THE FAUNA OF THE *TAPINOCEPHALUS* ZONE (BEAUFORT BEDS OF THE KAROO)

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(With 22 figures)

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Contents

A review of previous work on the *Tapinocephalus* zone and its fauna

The oldest record in print of the discovery of fossil bones in the rocks of the Karoo bears the date 1831. This is in the form of a letter printed in the *South African Quarterly Journal* — a letter signed by C. H. Crisbrook and addressed to Dr. Andrew Smith, Corresponding Secretary to the South African Institution. Crisbrook writes that while visiting Beaufort in 1827 he stayed with Mr. Baird, Ex-Landrost, who, amongst other mineral specimens, gave him a piece of a fossil tooth, which had been found by the son of Fieldcornet de Klerk.

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Crisbrook in the company of Baird, De Klerk and his son visited the site and found other specimens of which some were collected. There is no record of what became of these specimens nor can it with any degree of certainty be determined from Crisbrook's letter where the site was situated. The locality indications given are inadequate and in important points contradictory. Ruling out what would appear to be discrepancies I believe that these first specimens are from the *Tapinocephalus* zone within the Koup.

In any case, if not from the *Tapinocephalus* zone, these specimens are undoubtedly the first recorded Karoo fossils—antedating those found by A. G. Bain near Fort Beaufort by 11 years.

In the same publication mention is also made of 'Specimens of Fossil Bones of a large Mammiferous Animal from the Karoo; presented by the Rev. Dr. Adamson'. These most probably also came from the *Tapinocephalus* zone, but the data available are less convincing than those of the De Klerk discovery.

The A. G. Bain specimens received by the British Museum in 1853, although mostly from higher zones, do include some specimens from the Great Karoo. These are rather poor specimens but they undoubtedly are all dinocephalians from the *Tapinocephalus* zone. Lydekker (1890) considers that the British Museum specimen R1708 figured by Owen as *Tapinocephalus atherstonei* was also presented by A. G. Bain, 1853.

In a letter dated 18 January 1856 A. Rose-Innes of Beaufort West writes that he is sending by 'mail cart' two fossils to the South African Museum. There is no further record of these specimens and they may, of course, have come from either the *Endothiodon* or *Cistecephalus* zones exposed near Beaufort West.

In the following year, 1857, according to the museum register, Dr. Way presented the proximal end of a tibia. This specimen from Uitkyk is still in the collection of the South African Museum bearing the number 737 and was identified in 1955, thus nearly a century later, by Boonstra as a tibia of the titanosuchian reptile, *Jonkeria ingens*.

For the next 14 years no record could be traced of any work in the *Tapinocephalus* zone. Then in 1871, with the discovery of gold in the district of Prince Albert, the area becomes geologically important and at least two of the investigators of the mineral possibilities were also interested in fossils, viz. Dr. Atherstone and T. Bain. In a parliamentary report of that year Atherstone and Bain mention the occurrence of fossil bones on the farms Varsfontein, Spreeufontein and Janwillemsfontein. In the *Cape Monthly Magazine* Atherstone again refers to this area.

These specimens mentioned in 1871 were collected by Atherstone and sent to London, where they were shortly afterwards described by Sir Richard Owen in his *Catalogue of the fossil remains of Reptilia of South Africa*, and one constitutes the type of *Tapinocephalus atherstonei*, and another is the type of *Bradysaurus bombidens*. Another specimen was erroneously referred by Owen to

his 'Pareiosaurus' but subsequently made the type of *Phocosaurus megischion* by Seeley in 1888. Other specimens also referred to his 'Pareiosaurus' by Owen are really bones of a titanosuchid.

This confusion with respect to the bones collected by Atherstone appears to be mainly due to the fact that Atherstone did not keep his various finds separately but lumped bones derived from an area together to constitute a single specimen and this initial mistake was apparently aggravated by faulty labelling in the British Museum.

The collection which the British Museum purchased from T. Bain in 1878 includes specimens from the *Tapinocephalus* zone. A bone (49389) described by Seeley in 1889 as an ulna is really a tibia of *Titanosuchus*. Another specimen from Koedoeskop was made the type of *Titanosuchus ferox* by Owen in 1879. Fragments (49404) from Palmietfontein constitute Broom's type (1905) of *Cyniscodon lydekkeri*. It also includes the Palmietfontein specimen of *Bradysaurus bombidens* described by Seeley in 1888. No. 49425 was described by Seeley as the type of *Glaridodon*, but referred to *Titanosuchus* by Lydekker in 1889. A specimen from Letjiesbos (49407) has been referred to *Lycosaurus* (Boonstra 1934*a*).

In 1880 the British Museum purchased a further collection from T. Bain. A specimen from Vindraersfontein (R848) is the proximal end of a femur of *Brachypareia*. Five other specimens from the Koup are poorly preserved elements of Dinocephalia. R872 was made the type of *Hyorhynchus platyceps* by Seeley in 1889.

In 1881 H. W. Oakley, assistant at the South African Museum, was sent to the Koup on receipt by the museum of reliable information of the occurrence of fossil bones in that area. The results of this mission were mentioned in the *Report of the South African Museum* for 1881. Numerous fragmentary remains were found and these were entered as 'Fossil Bones of *Dicynodon*', but in the register and in the present collection only one specimen—a femur (739)—is preserved, identified in 1955 by Boonstra as that of *Titanosuchus*. A further result of Oakley's mission was that on his reporting hearsay evidence of the occurrence of further skeletons the Colonial Government in its budget for 1882–3 voted a sum of £200 for collecting Karoo fossils. With these funds available T. Bain was employed to collect for the South African Museum in the *Tapinocephalus* and higher zones in 1883. But before Bain's collecting trip the museum, according to the register, received from J. R. Joubert a collection of 11 specimens, all from 'near Beaufort West'. From this collection the types of *Ictidosaurus angusticeps*, *Scymnosaurus ferox*, *Dicynodon jouberti*, *Pristerodon brachyops* and *Dicynodon pseudojouberti* were later described by Broom (1903*b*, 1905*a*) and Boonstra (1948*b*). The collecting trip undertaken by Bain in 1883 on behalf of the museum was not a very successful undertaking and the museum today possesses only two specimens which were probably obtained by Bain. Only one, later described by Seeley as *Delphinognathus conocephalus*, is from the *Tapinocephalus* zone.

In 1884 Dr. Exton presented to the British Museum a flattened tibia (R519) which may be tapinocephalian

In 1888 Seeley published his account of *Pareiasaurus* (now *Bradysaurus*) *bombidens* based on the Palmietfontein specimen, which T. Bain had sold to the British Museum in 1878. A number of bones from Varsfontein, by Owen thought to be pareiasaurian, were in this paper by Seeley made the type of *Phocosaurus megischion*.

In 1889 Seeley erroneously described as a pubic bone a coracoid of *Titanosuchus* from Koedoeskop and also correctly a humerus, femur and fibula; from Varsfontein a titanosuchid ulna and from Janwillemsfontein he figured the tibia thought by Owen to be pareiasaurian and now considered titanosuchian.

In the same year Seeley visited South Africa, thus being the first trained vertebrate palaeontologist to collect personally in the Karoo. He spent some time collecting in the *Tapinocephalus* zone where he was accompanied by T. Bain. At Tamboerfontein he was given a skeleton by J. S. Marais, now known as the Tamboer specimen of *Bradysaurus bombidens*. Later Sarel Marais guided Seeley to another skeleton now known as the De Bad specimen of *Bradysaurus baini*. This specimen was excavated with the help of T. Bain, J. S. and Sarel Marais and their respective sons on 12 August 1889. In the *Transactions of the South African Philosophical Society* Seeley pays very warm tribute to the help he received from all the local farmers—his specimens were taken to the station by mule-wagon. A couple of sentences are here quoted. 'The Dutch farmers, ever on the alert for natural history phenomena, . . . at the first indication that we were likely to visit a certain spot, every specimen that could be in any way of interest to us was obtained, so that our labours were very much lightened' and further on, 'This carrying away was perhaps a little more difficult than we in Cape Town had imagined. We were in the open veldt, where there is no possibility of getting assistance . . . ; there are few facilities for bringing away the specimens in the best possible condition, but owing to the aid which was never wanting and never grudged in the least, we were able to gather up the fragments, which filled several large cases, and a procession of mule wagons bore away . . .'.

Every palaeontologist who has collected in the Koup will fully endorse this warm tribute of Seeley's.

In addition to the above, Seeley obtained from L. Pienaar of Weltevreden a specimen described in 1892 as the type of *Eunotosaurus africanus*. A specimen from De Cypher was made the type of *Pnigalion* by Watson in 1914 and another from Tamboerfontein became the type of *Anteosaurus*.

Lydekker in his *Catalogue* of 1890 listed and sorted out the specimens then in the British Museum, correcting a number of errors with regard to specimens from the *Tapinocephalus* zone.

In 1892 Seeley described the type of *Delphinognathus conocephalus*, which he had on loan from the South African Museum. This dinocephalian is thus the

oldest described type of Karoo vertebrate housed in a South African institution.

In 1895 Seeley described *Pristerognathus polyodon* collected by himself at Tamboerfontein in 1889, and in the same year published a photograph of the mounted De Bad specimen of *Bradysaurus baini*. In a book entitled *Creatures of other days* by Hutchinson, published in 1896, there is a drawing by J. Smit of *Bradysaurus baini* reconstructed in the 'flesh'. As the pose follows that of the Seeley's mounted skeleton the result is most unsatisfactory, but the drawing in Swinton's book (1948), half a century later, with the same pose, is inexcusable.

In the first annual report of the Geological Commission, 1896, Schwarz writes: 'In the lower beds of the Gouph a large quantity of *Pareiasaurus* bones were discovered, all of them referred to *P. Bainii*, but owing to the absence of facilities for excavating them they were left till more favourable circumstances should occur, one bit only, consisting of 16 vertebrae with the pelvis *in situ*, was taken for the sake of identification. . . . I have found them all over the country from Spreeufontein, Prince Albert, to directly under the Nieuweveld Mountains, as at Hottentots River and Knoflock's Fontein, and the same species occurs throughout. Just south-east of Fraserburg Road Station I have, however, obtained *P. bombidens*, Owen, and at the Prince Albert Goldfields a variety of large forms, some of which are new. *P. Bainii* is the commonest form.' In 1898 Webster presented some *Bradysaurus* vertebrae, found by him near Prince Albert Road, to the South African Museum.

From August 1902 Rogers and Schwarz spent over three months in the Koup. Rogers (1903) writes: 'During our journey in the Gouph, we heard of a large skeleton in the rocks near van der Byl's Kraal, and when we reached that place we found that the skeleton was on Hoogeveld, Lot A, ground which now belongs to Mr. J. P. Snyman, of Knoflock's Fontein. Mr. Snyman very kindly took us to the spot where the bones lay, and allowed us to remove them. In the matter of the transport of these bones, which weighed some 700 lbs., to our camping place, and thence to the railway, we were greatly helped by Mr. M. van den Bergh, of van der Byl's Kraal. . . . The bones were . . . cleared of their matrix by Miss Wilman, under the superintendence of Dr. Broom, who found that they are an almost complete skeleton of *Pareiasaurus serridens* . . . Owen.' (Now the type of *Embrithosaurus schwarzi*.) 'The Commission decided to have the fossils, collected since the commencement of the survey in 1896, named and described . . . and to have the descriptions published in a special volume of the Annals of the South African Museum'.

Rogers & Schwarz (1903) mention that many fragmentary bones were encountered. The better examples collected were examined by Dr. Broom. These are: from Grootfontein a small species of *Pareiasaurus*, from Buffel's Vlei an interclavicle probably of *Titanosuchus*, from Drooge Fontein a new fossil reptile – possibly allied to *Titanosuchus*, from possibly Knoflock's Fontein (per J. P. Snyman), the type of *Glanosuchus macrops* and from Paarde Bosch a partial humerus possibly of *Lycosaurus*.

In 1903 Broom described a skull, presented by the Rev. van der Merwe to the Victoria College (now the University of Stellenbosch), with the designation *Lycosuchus vanderrieti*. In the same year Broom described what is now the type of *Embrithosaurus schwarzi*, collected by Rogers and Schwarz (S.A.M. 8034), also *Titanosuchus cloetei* from the 'Gamka River' presented to the South African Museum by Mr. Justice Cloete; and the 1881 J. R. Joubert's types of *Ictidosaurus angusticeps* and *Scymnosaurus ferox*.

In their report for 1903 Rogers & Du Toit announce the discovery at Knechts Banken near Calvinia of 'Lamellibranch shells and fish scales, together with *Glossopteris*'; the first two were identified as *Palaeomutela* and *Palaeoniscus*. This locality is probably in Ecca beds. In his contribution to this report Schwarz mentions (p. 92) some localities where bones have been found, viz. Prince Albert Road Station, Spreeufontein, Kleinwaterval and Seekoeigat.

Also in 1903 the South African Museum received a collection from J. M. Bain which had been collected by his father, T. Bain; this includes, besides the type of *Pristerognathus baini*, four specimens of *Dicynodon jouberti*, one of *Robertia broomiana* two of ?*Titanosuchus* and a pareiasaurian bone. The latter is from Springfontein and all the others have the locality unrecorded. From C. de Villiers came a dinocephalian femoral fragment from Spes Bona, 23 miles south of Beaufort West.

In 1904 Broom collected the type of *Dicynodon megalorhinus* and P. H. du Plessis discovered at Seekoeigat the bones which Broom designated as the type of *Scapanodon duplessisi*.

In 1905 the Rev. J. H. Whaits, a railway clergyman and then rector at Prince Albert, discovered his first specimen, a *Lycosuchus*, in the *Tapinocephalus* zone at Fraserburg Road. In the same year P. H. du Plessis discovered at Seekoeigat specimens which became the types of *Alopecodon priscus* and *A. rugosus* and also two *Pristerognathus*, one *Glanosuchus*, one *Dicynodon megalorhinus*, seven poor dinocephalian specimens and fish scales. On Bokfontein he found what became the type of *Pelosuchus priscus* and on Waterval a poor skull of *Alopecodon*. Mr. J. L. Cairncross, operator of a drilling machine, discovered on Sandvlakte the specimens Broom made the types of *Eccasaurus priscus* and *Archaeosuchus cairncrossi*, incorrectly maintaining that they came from the Ecca beds, whereas in fact they are forms from the *Tapinocephalus* zone. At Prince Albert Road Station Cairncross also found fish scales and a skull of *Dicynodon pseudojouberti*.

In 1905 Rogers in his classification of the Karoo rocks retains Seeley's (1892*c*) triple division but calls them the Lower, Middle and Upper Beaufort beds. Broom (1905*b*) retains the name *Pareiasaurus* zone for the lowest part of the Lower Beaufort and proposes that the middle part be called *Endothiodon* zone and the upper zone *Kistecephalus* zone.

In 1906 Cairncross found a *Palaeomutela* and some poor pareiasaurian and dinocephalian bones near Prince Albert Road, and Whaits discovered the type specimens of *Trochosaurus acutus* and *Hyaenosuchus whaitsi* at Rietfontein,

Prince Albert and of *Pardosuchus whaitsi* and *Rhinesuchus whaitsi* at Fraserburg Road, together with a specimen of *Pristerognathus* at Rietfontein, Prince Albert, and at Fraserburg Road a specimen of *Cynariognathus paucioridens* and a tapinocephalian at Fraserburg Road. The above types were designated as such by Broom in 1908.

In 1907 Broom listed 16 types occurring in the *Pareiasaurus* (now *Tapinocephalus*) zone.

In 1908 Whaits contributed an *Eunotosaurus* from Rietfontein, Prince Albert, a *Jonkeria* from Letjiesbos and some pareiasaurian and dinocephalian fragments from Prince Albert Road. In 1909 A. R. E. Walker, of the South African Museum, collected at Roggekloof, Sutherland, the specimen made the type of *Pristerognathoides roggeveldensis* by Boonstra and also a *Bradysaurus* and some dinocephalian bones. He also excavated a pareiasaurian found by Gordon on his farm Hottentotrivier. In this year Broom (1909*a* and *c*) listed 20 species in the *Pareiasaurus* (now *Tapinocephalus*) zone and described as *Tapinocephalus* the skull in the Seeley collection, which Watson in 1914 made the type of *Mormosaurus seeleyi*.

Rogers in 1910 again worked for months in the *Tapinocephalus* zone in the districts of Beaufort West, Fraserburg, Sutherland and Laingsburg and the sheet map 13, commenced by Schwarz in 1896, was published. In the report of the Geological Commission for this year only one specimen from the *Tapinocephalus* zone is mentioned, viz. an *Alopecodon* from Skaapskooi, south-west of Fraserburg, together with fragmentary pareiasurian remains from the Moordenaar's Karoo and Komsberg.

Broom, in 1910, published his important comparison of the Permian reptiles of North America with those of South Africa; and also described a skull in the British Museum collected by Seeley at Tamboerfontein as a *Titanosuchus* (now the type of *Anteosaurus magnificus*).

In 1911 Broom described the type skull of the *Moschops* material found by Whaits on Spitzkop, Moordenaars Karoo and subsequently sold by Broom to the American Museum of Natural History and also *Eriphostoma microdon* found by Whaits near Fraserburg Road.

During 1912 the good skull and limb-bones of *Tapinocephalus* (S.A.M. 2343) were collected at Uitkyk by P. le Roux, M.P. for Beaufort West. Broom (1912*b*) designated as types of *Taurops macrodon* a snout found at Bosmanshoek in the Komsberg by Whaits and *Pristerognathus* (now *Cynariognathus*) *platyrhinus* from Grootfontein, Beaufort West. During 1912 Watson, with the help of a grant from the Percy Sladen Fund, collected in the Karoo using for conveyance, what Haughton describes as 'a decrepit horse and trap—the former capable at most of 10 miles per day'. Two of the important specimens which Watson collected in the *Tapinocephalus* zone—an *Embrithosaurus* skull and the type of *Broomia perplexa*—both came from Hottentotsrivier, Beaufort West.

In 1913 Haughton undertook his first collecting in the *Tapinocephalus* zone. On Abrahamskraal he collected the types of *Galesuchus gracilis* and *Trochosaurus*

intermedius and also a specimen of *Dicynodon jouberti*. On Uitkyk he obtained a *Brachypareia*. Working with Whaits two specimens of *Anteosaurus* and a tapinocephalian were collected at Vivier. Whaits found the type of *Struthiocephalus whaitsi* at Vivier.

In this year Broom described three specimens obtained for the Albany Museum by Whaits on Hottentotsrivier as the types of *Pareiasaurus* (later *Koalemasaurus*) *acutirostris*, *Scylacognathus parvus* and *Scymnorhinus* (now *Broomiasaurus*) *planiceps*. In the *Annals of the South African Museum* Broom also described a pareiasaurian manus and pes found by G. Gordon on Hottentotsrivier and excavated by A. R. E. Walker in 1909. In the same year Haughton published photographs of the skull of *Tapinocephalus* found by Le Roux on his farm Uitkyk in 1912. Watson (1914*b*) also published a paper on the Beaufort beds.

Broom, in 1914, wrote his important comparison of the South African dinocephalians with the American pelycosaurs and designated as the type of *Moschognathus whaitsi* a specimen that had been collected by Whaits in the Beaufort West district. In the *American Museum Journal* Broom published photographs of *Bradysaurus whaitsi* and of a shoulder girdle of *Tapinocephalus atherstonei* now known to be that of a titanosuchian. In his Croonian lecture Broom figured postcranial bones of *Moschops* and *Moschognathus* and listed 19 genera of tetrapods derived from the '*Pareiasaurus*' zone and erroneously two dinocephalian genera were said to be from the Ecca beds.

Watson published a number of papers in 1914 on his work in the *Tapinocephalus* zone. The first was on the *Embrithosaurus* skull he had obtained at Hottentotsrivier; the second on the zones of the Beaufort beds; the third on the nomenclature of the pareiasaurians in which he designates the specimen collected by Schwarz in 1902 as the type of *Embrithosaurus schwarzi*; the fourth paper was on the Dinocephalia, in which specimens in the British Museum were made the types of *Mormosaurus seeleyi*, *Pnigalion oweni*, *Lamiasaurus newtoni* and he also described a skull as *Titanosuchus* which he later made the type of *Anteosaurus magnificus*; in a fifth paper *Broomia perplexa* was described; sixthly, *Eunotosaurus africanus* was fully redescribed and lastly in a paper on the therapsids a specimen collected by T. Bain was described under the name *Lycosuchus*? (now *Scymnosaurus watsoni*.)

In 1914 Watson proposed that the lowest zone of the Beaufort beds be called the *Tapinocephalus* zone instead of *Pareiasaurus* zone.

During 1914 Haughton and Whaits collected together on Janwillemsfontein and obtained two specimens of *Bradysaurus seeleyi*, a humerus of *Jonkeria ingens*, a skull each of *Scymnosaurus ferox* and *Pristerognathus* and an unidentified therocephalian. Haughton excavated a skull and much of the skeleton of *Struthiocephalus whaitsi* on Abrahamskraal and from La-de-da he obtained the skull which became the type of *Moschosaurus longiceps*.

In 1915 Rogers collected a skull which has since been identified (Boonstra 1954) as *Pristerognathoides minor* on Jakhalsfontein, Prince Albert. Whaits collected the type of *Riebeeckosaurus longirostris* at Vivier Siding and at Prince

Albert Road he found a specimen of *Dicynodon jouberti* and an *Emydops longiceps*, at Klipbank the type of *Pristerognathoides minor*, at Letjiesbos a lycosuchid skull and on Brand Doorns (Leegte?) a titanosuchid jaw and a gorgonopsian and at Hottentotsrivier a lower jaw of *Brachypareia watsoni*. Haughton, in 1915, on Abrahamskraal obtained a skull of *Robertia broomiana* and fragments of an *Anteosaurus*, figured by Boonstra in 1955, and from Uitkyk brought the limb-bones associated with the *Tapinocephalus* skull that had been found by P. le Roux and also a beautiful moschopid fibula. Also in 1915 Broom published his catalogue of the specimens he had sold to the American Museum; this contained two pareiasaurs, eleven dinocephalian specimens, and six therocephalians, all of which had been found by Whaits.

Haughton in 1915 described the types of *Struthiocephalus whaitsi* (found by Whaits in 1913), and *Trochosaurus intermedius* and *Titanosuchus dubius* found by himself in 1913. Broom in 1915 named a number of poor specimens in the British Museum that had been purchased from T. Bain in 1878; the new names are *Simonhinella baini*, the paratype of *Ictecephalus polycynodon*, *Cerdodon tenuidens*, *Cyniscodon lydekkeri* and *Scymnosaurus watsoni*. In September of this year Haughton described a skull found by himself at La-de-da as *Moschosaurus longiceps* and another collected in 1913 at Abrahamskraal as *Galesuchus gracilis*.

In 1916 Van Hoepen described a skull and partial skeleton from Abrahamskraal under the name *Jonkeria truculenta*. During this year Haughton collected in the Koup and found at Abrahamskraal seven pareiasaurs, four dinocephalians and one therocephalian; on Leeurivier he obtained two pareiasaurs and four dinocephalians; on Bloukrans two dicynodonts, on Welgemoed the type of *Jonkeria haughtoni* and a good *Bradysaurus seeleyi*; on Stinkfontein a *Scymnosaurus ferox* and the type of *Alopecideops gracilis*; on Lammerkraal the type of *Struthiocephaloides cavifrons* and a poor titanosuchid; from Rietfontein another titanosuchid and from Rietkuil a *Koalemasaurus*. W. van der Byl also presented a skull which later became the type of *Bradysaurus vanderbyli*.

During 1917 Haughton spent two weeks in the Koup and obtained 16 pareiasaurs, nine dinocephalians, four therocephalians, two dicynodonts and on Voëlfontein and Bloukrans fish scales. Cairncross collected a *Dicynodon jouberti* at Prince Albert Road.

In 1918 Haughton described the specimen found by Whaits at Klipbank as *Alopecognathus* (now *Pristerognathoides*) *minor* and figured the braincase of a tapinocephalid which had been found by P. le Roux in 1905. In this year A. L. du Toit discussed the zones of the Karoo system. During 1919 Van der Byl collected a *Dicynodon jouberti* and an unidentified gorgonopsian and a dinocephalian and Haughton in his review lists 40 genera in the *Tapinocephalus* zone.

In 1920 Gregory published a notice of the mounted skeleton of *Moschops capensis* Broom and Joleaud proposed the name *Broomisaurus* for Broom's *Scymnorhinus*.

In 1921 Watson re-examined the type of *Scymnosaurus watsoni* and proposed

the name *Anteosaurus magnificus* for the specimen previously described as a *Titanosuchus*, and Broom reconsidered the tarsus of *Broomia perplexa*.

Romer, in 1922, in his paper on the locomotor apparatus, discussed the conditions in *Moschops* and *Propappus*. Abel in his *Lebensbilder* in 1922 discussed some palaeobiological aspects of life in the Karoo.

Broom, in 1923, described a skull referred to *Scapanodon duplessisi* collected by Van der Byl on Abrahamskraal, also two skulls from Kookfontein found by M. J. van Wyk were designated as the types of *Dinophoneus* (now *Jonkeria*) *ingens*, another skull found by Van der Byl on Abrahamskraal became the type of *Dinartamus vanderbyli* and a lower jaw was described as *Titanosuchus cloetei* (later this became the type of *Phoneosuchus* (now *Jonkeria*) *angusticeps* and a further jaw became the type of *Enobius strubeni*). Also during 1923 C. le Roux collected on Boesmanskop the types of *Dolichopareia angusta* and *Nochelesaurus alexanderi* and on Abrahamskraal the type specimen of *Brachypareia watsoni* and at Zwarts Siding an *Embrithosaurus schwarzi* and on Lammerkraal an unidentified therocephalian and on Bloukrans the type of *Pristerognathoides vanwyki*.

Haughton in 1923 accompanied Case on a journey through the Karoo on which the latter based some of the views expressed in his paper of 1926.

In 1924 Haughton accompanied Von Huene through the Karoo and the latter obtained specimens from the *Tapinocephalus* zone which are now housed at Tübingen, and described in 1931. Von Huene's observations during this trip were incorporated in his compilation of 1925. Haughton (1924*a*) also described as *Galesuchus gracilis* the specimen collected by himself on Abrahamskraal in 1913, and in his bibliographic list (1924*b*) he listed 56 species as definitely from the *Tapinocephalus* zone. In 1924 Broom described a young pareiasaurian skull found by Van der Byl on Abrahamskraal and a new species *Pareiasaurus* (later *Nochelesaurus*) *strubeni* from the same locality. C. le Roux collected in 1924 a *Dolichopareia angusta*, a *Pristerognathus* and a *Propappus* on Abrahamskraal.

In 1925 Broom described a skull found by Van der Byl at Abrahamskraal as the type of *Pristerognathus vanderbyli* and another became the type of *Alopecodon minor*; and from Lammerkraal *Ictipareia brevirostris* and the specimen collected for the South African Museum by C. le Roux on Bloukrans in 1923 became the type of *Pristerognathus* (now *Pristerognathoides*) *vanwyki*. In 1925 Haughton mentions a specimen of *Rhinesuchus whaitsi* from Bloukrans.

Von Huene's 'Lebensbild' (1925) was a very useful compilation of the then known facts on the fauna of the Karoo. It was palaeobiologically orientated and included a zone map—the first published—but being based on the inadequate survey of the area was inaccurate in many respects, in particular as far as the limits of the *Tapinocephalus* zone is concerned. The fauna of the *Tapinocephalus* zone was listed as consisting of one invertebrate, one fish, one stegocephalian, seven cotylosaurs, one archichelonian, 21 dinocephalians, three dromasaurians, three dicynodonts, three gorgonopsians, 21 therocephalians, one cynodont? and three incertae sedis. This makes a total of 66 species.

Rogers in 1925 published a sheet map with an explanation of the country near Laingsburg and mentions only three localities of fossil finds.

In 1926 Haughton in an address, 'Palaeontology in South Africa', listed 68 species from the *Tapinocephalus* zone. Gregory also published a detailed account of the skeleton of *Moschops* and also of some features of *Moschognathus* and reviewed the work on other described dinocephalians. In his study on the environment of tetrapod life, Case incorporated his observations made in the *Tapinocephalus* zone during 1923.

In 1927 Broom described the important skull of *Anningia megalops* found by Van der Byl on the farm Bloukrans, Prince Albert.

In 1928 Broom described the type skull of *Taurocephalus lerouxi* found by J. J. le Roux and his brother on Abrahamskraal and of *Criocephalus vanderbyli* found by Van der Byl on the same farm and he also figured a partial skull of *Tapinocephalus* found by M. J. van Wyk on Ganskraal, Prince Albert. Bones found by Haughton in 1917 on Sewefontein, Prince Albert, were in error figured as those of *Tapinocephalus*, whereas they are in fact titanosuchian (*Scapanodon septemfontis*).

In 1928 Boonstra, without any own means of conveyance and relying wholly on the friendly farm-owners for transport from farm to farm, started on a collecting trip from Beaufort West. On Boeteka he collected a partial femur of *Phocosaurus*; on Mierfontein an ilium and humerus of *Jonkeria* and a pareiasaurian humerus and ulnae; on Leeufontein two fair specimens of *Bradysaurus seeleyi*, on Boesmansrivier the type specimen of *Styracocephalus platyrhynchus* and three poor pareiasaurs; on Mynhardtskraal six pareiasaurs including the one which yielded the first completely preserved manus, and postcranial bones of a struthiocephalid and of *Keratocephalus*; and on Kleinkoedoeskop the type skull and skeleton of *Hipposaurus boonstrai*, a good *Nochelesaurus* skull and a pareiasaurian pelvis and a fibula of *Parascaponodon*. J. C. Avenant of Die Walle, part of Kleinkoedoeskop, was hired to take the specimens to Letjiesbos station and Boonstra got him interested in locating fossils. The result was that early in the following year Boonstra went up to excavate a number of fossils located by Avenant on Koedoeskop and on this trip some of the neighbouring farms were also worked with the help of Avenant's donkeycart. From Kleinkoedoeskop the specimens which later became the types of *Jonkeria koupensis*, *Scymnosaurus major* and *Robertia broomiana* were collected in addition to four pareiasaurs, eight dinocephalians, 40 dicynodonts, four therocephalians and a gorgonopsian; from Rietkuil were obtained what later became the type of *Pristerosaurus microdon*, a *Scymnosaurus* and a *Pristerognathus*, a gorgonopsian and three dinocephalians and from Boesmansrivier an *Anteosaurus* snout. Arrangements were then made to hire Avenant's donkey-wagon for a three-month trip commencing in March. This trip yielded the following: from Die Vlei a *Pristerognathus* and two other therocephalians; from Stinkfontein an *Alopecognathus* and another therocephalian; from Sewefontein a lower jaw of *Brachypareia watsoni*; from Voëlfontein the specimen which later

became the type of *Parascapanodon avifontis*, three *Bradysaurus seeleyi* with feet, a *Bradysaurus baini* and two *Embrithosaurus*, a good *Anteosaurus abeli* skull and six other dinocephalians, a *Scymnosaurus* and two fragmentary stegocephalians; from Seekoeivlei four *Bradysaurus* and two *Jonkeria haughtoni*; from Vindraersfontein a dinocephalian femur; from Boorfontein and Klipbanksfontein each a gorgonopsian; from Knoffelfontein a complete skeleton with feet of a *Bradysaurus seeleyi*; a *Bradysaurus vanderbyli*, *Brachypareia rogersi*, a pareiasaurian femur and a fair skull of *Scymnosaurus major* found by the owner, Snyman; from Kruisvlei the specimens which years later became the types of *Avenantia kruisvleiensis* and *Anteosaurus acutirostris* and in addition a *Bradysaurus seeleyi* and the mass entombment of cranial and postcranial elements of at least a dozen *Moschops* individuals. On the Merweville Commonage a femur of ?*Tapinocephalus* was found; on Melkbosfontein four *Bradysaurus baini*—one a giant with all four feet—were collected; on Welgemoed an *Embrithosaurus* with feet; on Wilgerfontein a poor pareiasaur and dinocephalian; on Saairivier the type humerus of *Jonkeria parva*; on Jacobskraal a tapinocephalid, a therocephalian and an amphibian; from Wolwefontein (Wakkerstroom) a paratype of *Parascapanodon avifontis*, two *Jonkeria*, a tapinocephalian and a moschopid, two pareiasaurians and a scylacosaurid were collected.

Rietfontein, Prince Albert, yielded a beautiful moschopid fibula; Droëfontein a dinocephalian as also Elandskop; on the last farm worked, Veldmansrivier, a scapulo-coracoid of *Parascapanodon* and a skull of *Brachypareia? rogersi* were found.

In 1929 Broom in his review of the Titanosuchidae designated the following new types: *Jonkeria vanderbyli* for a specimen collected by Broom on Abrahamskraal, *Jonkeria crassus* for a poor specimen found by Van der Byl near Kruidfontein Station, *Dinosphageus* (now *Jonkeria*) *haughtoni* for a skull and some postcranial elements collected in 1916 by Haughton on Welgemoed, *Phoneosuchus* (now *Jonkeria*) *angusticeps* for a lower jaw found by Van der Byl on Abrahamskraal, *Jonkeria pugnax* (now *ingens*) for a skull found by M. J. van Wyk on his farm Kookfontein and *Anteosaurus* (now *Pseudanteosaurus*) *minor* found by Broom near Merweville.

Haughton (1929*c*) described the following therapsids: an imperfect skull found by Boonstra on Boesmansrivier was made the type of *Styracocephalus platyrhynchus*, a skull found by himself on Abrahamskraal in 1920 as *Eoarctops vanderbyli* and a second gorgonopsian *Hipposaurus boonstrai* has as type specimen a skull of the nearly complete skeleton collected by Boonstra on Kleinkoedoeskop.

In the same part of the *Annals of the South African Museum* Haughton & Boonstra attempted a classification of the Pareiasauria and the following new names were proposed for forms from the *Tapinocephalus* zone: *Bradysaurus seeleyi* and *Bradysaurus vanderbyli*, *Bradysuchus* (now *Bradysaurus*) *whaitsi*, *Nochelesaurus alexanderi* and *Pareiasaurus strubeni* became *Nochelesaurus strubeni*, *Dolichopareia angusta* and *P. acutirostris* became *Koalemasaurus acuticostris*, *Brachypareia watsoni* and in this new genus was also placed the former *Propappus*

rogersi and lastly *Platyorpha broomi.*

Haughton (1929*b*) also described the braincase in a number of pareiasaurs.

Boonstra in two further papers in the series of 'Pareiasaurian studies' described the first complete manus in the specimen of *Bradysaurus vanderbyli* collected by himself at Mynhardtskraal and some incomplete pedes.

In December 1929 Broom figured the shoulder girdle of *Pristerognathoides minor.*

During 1929 two major scientific conferences were held in South Africa, viz. the joint meeting of the British and the South African Associations for the Advancement of Science and the XV International Geological Congress. Before, during and after these meetings some of the visiting palaeontologists collected in the *Tapinocephalus* zone. They were W. Janensch of Berlin, Othenio Abel of Vienna and A. S. Romer with the veteran American collector Paul Miller as his assistant, whereas D. M. S. Watson was more interested in the younger zones.

Abel, spending a few days under the guidance of L. D. Boonstra, obtained a few bones of pareiasaurs and dinocephalians and a paper published in 1930 contained nothing new. Romer and Miller worked from two camps – Stinkfontein and Hottentotsrivier. I quote two paragraphs of a letter from Romer giving his views on the nature of *Tapinocephalus* zone matrix and collecting in it:

> 'We found collecting in the Tapinocephalus zone pleasant and comparable in many ways to conditions in our western states. We camped out, with a cook and general camp helper. The terrain in the zone is relatively flat, and fences few, so that, much as in many western areas, we found little difficulty in reaching any locality by car – particularly useful in picking up ponderous pareiasaur or dinoceph materials. The roads were few and poor – parts of the Main Cape to Johannesburg road were no more than a pair of ruts in the veldt, if that – but that, again, was a familiar condition in our own West at that time. The local farmers were friendly and cooperative. And the total lack of rainfall during our visit to the Gouph was, of course, a boon to the collector (although not to the sheep farmer).
>
> The one great disadvantage to collecting in this zone is, of course, one with which you are all too familiar, but for which we were not fully prepared – the exceedingly hard nature of the mudstone matrix. I remember all too well our first day in camp at Stinkfontein. Miller and I set out to prospect in the morning and met again for lunch. Both of us had seen an excellent fossil prospect, and went out in the afternoon to develop our finds. When we met again for supper, both of us were exceedingly discouraged. We ruined our chisels, dulled our picks, and made almost no impression on the rock!'

A list supplied by D. Techter gives the 'booty' taken to Chicago as: about a score each of Dinocephalia and Pareiasauria, three Amphibia, at least six

Therocephalia and a number of anomodonts. Except for a few described by Broom and Olson (*Struthiocephalus milleri* and *Rhinesuchoides tenuiceps*) and *Moschoides romeri* (Byrne) and *Brachyprosopus broomi* Olson and some studied, but specifically unidentified by Olson, 'the vast bulk of the material has never been studied, catalogued, or even adequately prepared' (letter dated 24 May 1956 from D. Techter to the author).

Janensch collected for the Paläontologisches Museum of the Humboldt University in Berlin the following specimens: seven pareiasaurs, three dinocephalians and two therocephalians.

In 1930 Broom published a figure of *Scylacognathus parvus*.

Boonstra's study of the pareiasaurian mandible was published as a joint paper with Haughton and the material studied included 27 specimens from the *Tapinocephalus* zone. Later in the same year Boonstra's work on the pareiasaurian hind-limb was again published as a joint work with Haughton and was based on 26 specimens from the *Tapinocephalus* zone and some from younger zones.

Haughton's paper before the International Geological Congress included a discussion of the fauna of the *Tapinocephalus* zone.

In 1931 Von Huene's paper appeared in which he gave an account of the most important specimens he had collected in 1924. The *Tapinocephalus* zone forms described were: the type specimen of *Keratocephalus moloch* from Abrahamskraal; the type skull of *Dicynodon haughtonianus* from Bloukrans and further a skull of *Bradysaurus baini* and a lower jaw of *Nochelesaurus strubeni*, both from Abrahamskraal, as also postcranial bones of a *Jonkeria* and tapinocephalids and lastly ten specimens of *Dicynodon jouberti* and four of *Dicynodon megalorhinus*, all from Bloukrans.

In 1931 Broom proposed the new generic name, *Cynariognathus*, for the specimen in the American Museum collected by Whaits on Grootfontein, Beaufort West, previously described as *Pristerognathus platyrhinus*.

In 1931 Boonstra, travelling over the *Tapinocephalus* zone, managed to collect the type of *Alepognathus angustioriceps* on Kroonplaas, a pareiasaurian humerus on Boesmansrivier, some dicynodonts on Kroonplaas and a struthiocephalid scapula on Grootfontein in the Fraserburg district. In the same year Van der Byl presented a *Criocephalus* skull from Abrahamskraal to the South African Museum. In 1932 a partial skull of *Keratocephalus moloch* was obtained from Fraserburg Road.

In February, 1932, Boonstra's account on the fore-limb of the pareiasaurs was published which included reference to 12 specimens of *Bradysaurus baini*, seven of *Bradysaurus seeleyi*, three of *Bradysaurus vanderbyli*, six of *Bradysaurus* sp., one of *Platyorpha*, one of *Nochelesaurus strubeni* and two of *Nochelesaurus alexanderi*, three of *Dolichopareia angusta*, five of *Embrithosaurus schwarzi*, and four of *Brachypareia*. Hans Reck collected in the Koup during 1932.

In October, 1932, Boonstra published on the palaeobiology of and the divergence in the Pareiasauridae and on the hyoid apparatus in the Pareia-

sauria. In the same year Broom's *Mammal-like reptiles of South Africa* was published by Witherby and in this book the following *Tapinocephalus* zone forms were included: one anningiamorph, 32 dinocephalians, 33 therocephalians, two dromasaurians, six gorgonopsians, one burnetiamorph and three anomodonts.

During 1933 Boonstra wrote on the distribution of the pareiasaurians in the Koup and on a method used in the excavation of these reptiles.

In the same year Grossarth collected for the Alte-Akademie in Munich.

In April, 1934, Boonstra described the cranial osteology in the series of pareiasaurian studies in which 49 skulls from the *Tapinocephalus* zone were studied. This was followed by an account of the dermal armour and the vertebral column and ribs. In the whole series of pareiasaurian studies the various specimens were assigned to a stratigraphic position within the zones, viz. low, mid and high, and this was done on the then prevalent idea that the rocks in the Koup were lying in the main horizontally and that the present day topography indicated the stratigraphic position. Rossouw & De Villiers's work (1952) have since shown that this was false.

In June, 1934, Van Hoepen, in his paper on the classification of the Dicynodontia, proposed new generic names for some of the forms from the *Tapinocephalus* zone – but these have not been accepted by later workers and fall away.

In July, 1934, Boonstra published three papers in the *Annals of the South African Museum*. The first (1934*a*) included an account of the postcranial skeleton of *Hipposaurus boonstrai* found by himself in 1928; the second (1934*b*), on the Gorgonopsia in the British Museum, included a re-study of the type of *Cyniscodon lydekkeri*; and in the third paper (1934*c*) the following Therocephalia from the *Tapinocephalus* zone in the British Museum were re-examined: *Alopecodon*, *Cynariognathus*, *Pristerognathus*, *Scylacosaurus*, *Scymnosaurus*, *Trochosaurus*, *Cerdodon*, *Ictecephalus* and the doubtful *Hyorhynchus* and *Theriodesmus*.

Towards the end of 1934 Broili & Schröder described a gorgonopsian specimen found by Grossarth in the previous year on La-de-da and made this skull the type of *Pachyrhinos kaiseri*.

During January, 1935, Boonstra published three papers in the *American Museum Novitates* on specimens in the American Museum. In the first it was proposed that Broom's *Pareiasaurus whaitsi*, later made the genotype of *Bradysuchus* by Haughton and Boonstra, be considered a species of the genus *Bradysaurus*; in the second paper the following Therocephalia from the *Tapinocephalus* zone were re-studied: *Alopecodon*, *Alopecognathus*, *Cynariognathus*, *Scylacorhinus falkenbachi* synonym of *Scylacosaurus sclateri* and *Trochosaurus* and thirdly a new account was given of the type specimen of the gorgonopsian, *Eriphostomna microden*.

During 1935 Broili & Schröder published two papers in which specimens from the *Tapinocephalus* zone are described: from Brakwater, Schröder brought a dinocephalian, which was named *Titanognathus* (now *Anteosaurus*) *lotzi*; in

the second paper a new form of endothiodont, *Brachyuraniscus reuningi*, from La-de-da, collected by Grossarth in 1933, is described.

In October, 1935, Broom described *Lycedops scholtzi*, collected by C. S. Scholtz on Abrahamskraal and in 'Notes on some species of pareiasaurian reptiles' he wrote about the forms from the *Tapinocephalus* zone. Finally, in 1935 Boonstra collected a pareiasaurian skull on Voëlfontein.

Early in 1936 Broili & Schröder described *Cynariognathus seeleyi* on a skull found by Grossarth in 1933 on the farm La-de-da.

In May, 1936, Broom described a skull found on Stinkfontein under the name *Dinosuchus* (now *Anteosaurus*) *vorsteri*, a snout found by Van Hoepen on Abrahamskraal many years before became the type of *Dinopolus atrox*, and an imperfect skull was made the type of *Trochorhinus vanhoepeni*. A skull found by Broom at Letjiesbos was figured as that of *Pristerognathus baini*, and a specimen discovered by J. A. Galloway at Luttig became the type of *Cynariognathus gallowayi*.

In August, 1936, Boonstra redescribed both the tapinocephalian and the titanosuchian cranial material housed in the American Museum. In September Broom (1936*a*) gave a fuller description of *Dinosuchus* (now *Anteosaurus*) *vorsteri*. In November Broili & Schröder described a skull found by Grossarth on Klein-Waterval under the name *Pristerognathus peyeri*.

In the *Philosophical Transactions* Broom figured sections through a number of therocephalian skulls including that of a new species — *Trochosaurus dirus*.

During 1936 Camp collected in the Koup but I have not been able to get a list from him of the specimens collected.

In June, 1937, Broili & Schröder described some anomodont skulls that had been collected by Grossarth on La-de-da under the name *Dicynodon* (now *Oudenodon*) *huenei* and synonyms of this species under the names *Dicynodon broomi* and *D. grossarthi*. In September Broom (1937*b*) described the skull of *Elliotsmithia longiceps* which had been obtained in about 1917 by Van Hoepen from Abrahamskraal, and a skull from Grantham as *Struthiocephalus rheederi* and thirdly a skull from Klipbank under the name *Dicynodon gamkaensis*.

In October, 1937, Olson & Broom described some specimens in the Walker Museum, Chicago, that had been collected by Romer and Miller in 1929, viz. a skull of *Struthiocephalus milleri* and one of *Rhinesuchoides tenuiceps*, both from Stinkfontein.

In November Broom (1937*a*) gave the name *Alopecognathus megalops* to a skull found by Van der Byl in 1929 on Abrahamskraal.

In December Olson fully described a skull collected by Romer and Miller on Hottentotsrivier under the name *Brachyprosopus* (now *Brachyuraniscus*) *broomi*. Also in 1937 Byrne named a skeleton collected by Romer and Miller on Hottentotsrivier in 1929 *Moschops romeri*.

Finally in 1937 Boonstra collected the types of *Anteosaurus major* on Boesmansrivier and of *Anteosaurus abeli* on Kruisrivier in the Sutherland district.

In July, 1938, Olson sectioned and described an unidentified thero-

cephalian skull collected in 1929 by Romer and Miller on Sewefontein.

During 1938 Boonstra, collecting in the Koup, found on Deesweesfontein the type skull of *Koupia koupensis* and limb bones of *Phocosaurus*; on Buffelsvlei a paratype of *Anteosaurus crassifrons* and three tapinocephalids, a pareiasaurian skull on Skoppelmaaikraal, and on Boesmansrivier a pareiasaurian skull, a femur of *Phocosaurus* and some limb-bones of *Parascapanodon*.

During May, 1939, Boonstra collected on Buffelsvlei five therocephalians belonging to the genera *Pristerognathus* and *Scymnosaurus* and a *Glanosuchus macrops*, a *Dicynodon pseudojouberti* and a weathered titanosuchian skull; from Koedoeskop a *jonkeria haughtoni*; from Bloukrans per P. J. Rossouw a *Dicynodon jouberti* and a *Bradysaurus* skull from Mynhardtskraal.

In December, 1939, Boonstra published his review of a century of work on the Karoo.

In 1940 Von Huene included in a compilation the then known forms from the *Tapinocephalus* zone, viz. one labyrinthodont, 13 Pareiasauria, one archichelonian, three anningiamorpha, 21 titanosuchids, 15 tapinocephalids, two dromasauria, 30 pristerognathids, three alopecopsids, two ictidosuchids, two scaloposaurids, nine Gorgonopsia, one burnetiamorph, nine anomodonts and *Tamboeria maraisi*. In 1940 Boonstra described *Rhinosuchus avenanti* from a skull found by Avenant on Mynhardtskraal. Romer & Price in their 'Review of the Pelycosauria' included the following forms from the *Tapinocephalus* zone in the Varanopsidae? – *Elliotsmithia* and *Anningia*, and Byrne made some comparisons of his *Moschoides* with other therapsids.

Finally during 1940 Boonstra collected on Mynhardtskraal the type of *Paranteosaurus primus*, *Anteosaurus levops*, a paratype of *Parascapanodon avifontis*, a good *Bradysaurus seeleyi* skull, a juvenile *Struthiocephalus whaitsi*, a femur of *Titanosuchus ferox*, two *Jonkerias* and a *Galesuchus*; on Cypher some therocephalian limb-bones, parts of an endothiodont and a *Dicynodon jouberti*; on Voëlfontein a *Bradysaurus*; on Kroonplaas the type of *Cynariognathus paucioridens* and nine dicynodonts and on Kleinkoedoeskop four *Jonkerias*, one *Anteosaurus abeli*, a *Struthiocephalus whaitsi*, a *Pristerognathus* and four dicynodonts; on Bulwater a good skull of *Anteosaurus vorsteri*; on Buffelsvlei a *Struthiocephalus*, a *Struthiocephaloides* and a moschopid femur and from A. C. Bothma of Die Krans he obtained a new species of *Moschops* and from Aasvoëlbos a *Scapanodon septemfontis*.

In 1941 Broom reconsidered the position of *Broomia* and *Eunotosaurus* and H. Zinn collected a specimen of *Dicynodon pseudojouberti* from Dikbome in the Laingsburg district.

In March, 1942, Watson in a review of the Permian and Triassic tetrapods discussed the dinocephalians of the *Tapinocephalus* zone. In November Camp, Taylor & Welles proposed for *Dinosuchus* the name *Broomiasuchus* but this skull really is a species of *Anteosaurus*. Von Huene suggested that the vertebra described by Seeley under the name *Tamboeria maraisi* may be that of a pristerognathid therocephalian. During a short collecting trip in 1942 Boonstra collected

on Dikbome the type skull of *Anteosaurus laticeps* and a skull of *Struthiocephalus whaitsi*.

In a comparative paper on the cranial morphology of the therapsid suborders, Olson in 1944 studied the following skulls from the *Tapinocephalus* zone: two anomodonts from Hottentotsrivier and another two from Stinkfontein, of the former one is the geno-holotype of *Brachyprosopus* (now *Brachyuraniscus*) *broomi*, a therocephalian from Sewefontein and a pristerognathid from Hottentotsrivier. These specimens were all collected by Romer and Miller during 1929.

In 1945 Hesse collected the following specimens at Prince Albert Road: a *Pristerognathoides vanwyki*, a *Robertia broomiana*, a *Dicynodon pseudojouberti* and a *D. jouberti*.

During 1946 Boonstra collecting with the help of J. du Plessis, on Dikbome, the type skull of *Struthiocephaloides cavifrons* and, on Koringplaas in the Laingsburg district, the type skull of *Anteosaurus cruentus*. In the Sutherland district Boonstra obtained from Esperance a *Robertia broomiana* and a *Dicynodon pseudojouberti*, and on Elandsberg a *Dicynodon pseudojouberti*, two tapinocephalids and an unidentified tapinocephalian; in the Fraserburg district on the farm Seleryfontein an unidentified therapsid and a *Dicynodon* were found and on both Rietfontein and Kookfontein a *Dicynodon jouberti*.

Boonstra in 1947 collected the following: on Dubbelfontein (Brits Eigendom) 58 *Dicynodon* skulls and two weathered therapsid skulls; on Lammerkraal through Mr. J. Pienaar, the owner, the type skull of *Agnosaurus pienaari* and in addition eight *Dicynodons*, a *Scymnosaurus* and four other therocephalians; from Veldmansrivier three gorgonopsians and a *Pristerognathus*; on Perdewater six skulls of *Pristerognathus* and 21 *Dicynodons*.

In 1948 Watson discussed certain cranial features of the tapinocephaloids and titanosuchids. In the same year Boonstra reviewed the anomodonts of the *Tapinocephalus* zone and erected the new genera *Robertia* and *Koupia* and the new species *Dicynodon pseudojouberti* and as the name was preoccupied, proposed that Broili & Schröder's *Dicynodon huenei* be named *D. broilii* (now *Oudenodon huenei*). Localities of all the specimens from the zone in the South African Museum are given. Boonstra in a semi-popular book gave an account of the *Tapinocephalus* zone and included reconstructed life scenes depicting *Bradysaurus seeleyi*, *Keratocephalus* and a titanosuchid and a tapinocephalian (executed by Hesse) and also a *Moschops* in the flesh.

Finally, in 1948, Boonstra collected the following specimens: on Bloukrans a paratype of *Parascapanodon avifontis*, on Steenboksfontein two *Dicynodons*; on Skroefpaal a good *Jonkeria* skull that had been located by Rossouw; on Michau's Request a mass of *Dicynodon* skeletons that had been located by Jooste; on Vindraersfontein the type of *Theroides cyniscus*, a *Jonkeria* and an *Anteosaurus*; on Bosluiskraal and Skoorsteen a number of *Dicynodons* and on Lammerkraal three skulls of *Pristerognathus*, one of which had been found by the owner, J. Pienaar. Boonstra also accompanied P. J. Rossouw, who was mapping the

area, to indicate the spots where previous finds had been made. Zinn also collected two *Dicynodons* on Dikbome. In 1948 the Geological Survey presented a tapinocephalian femur found at Arthurskraal—one of the most easterly localities of the *Tapinocephalus* zone that have yielded fossils.

In 1951 F. P. Grobbelaar presented a *Dicynodon jouberti* found at Fraserburg Road to the South African Museum. Boonstra described a skull of *Keratocephalus moloch* from Fraserburg Road which had been obtained in 1932, and to this is appended a note by Von Huene on the Tübingen specimen. Brink & Kitching described the snout of *Walteria skinneri* which came from the farm Elandsfontein.

Finally for this year Boonstra collected: on Dikbome a hind-limb with pes of *Bradysaurus* and five pristerognathids, on Steenboksfontein the type of *Ptomalestes avidus* a tibia of *Parascapanodon*, two therocephalians, two *Dicynodons* and a *Mormosaurus*; on Droëfontein a *Dicynodon* and an interclavicle of *Struthiocephalus*, on Bosluiskraal a *Pristerognathus*; on Buffelsvlei (assisted by J. Marais) the type of *Maraisaurus parvus*, a paratype of *Anteosaurus crassifrons*, a *Keratocephalus*, a *Dicynodon*, a moschopid and a *Pristerognathus*; on Vereniging a skull of *Brachypareia*; on Skoppelmaaikraal a *Pristerognathus*.

In 1952 Boonstra published a number of short papers in which were described: the type skull of *Struthiocephalus akraalensis*, *Hipposaurus major*, with a life-sized reconstructed model of *Hipposaurus boonstrai*, the type skull of *Anteosaurus abeli*, a redescription of the type skull of *Struthiocephalus whaitsi*, the type skull of *Struthiocephalus* (now *Struthiocephaloides*) *duplessisi*, the type skull of *Struthiocephaloides cavifrons*, the type skull of *Agnosaurus pienaari*, the type skull of *Riebeeckosaurus longirostris*, that of *Avenantia kruisvleiensis* and the type skull of *Struthionops intermedius*. Also in 1952 Rossouw & De Villiers published their sheet map of Merweville and the explanation thereto in which the known fossils occurring within the area mapped are listed with the localities of each indicated and the *Tapinocephalus* zone sub-divided into three horizons, with tables indicating the distribution of the fossils.

Boonstra in 1952 collected the following specimens: on Nuwefontein (Roxana) in the Nieuweveld a complete skeleton of *Bradysaurus seeleyi*, and a fair skull of *Anteosaurus abeli*, both located by Jooste; on Kruis van Bloemfontein a *Eunotosaurus* picked up by F. D. Visser; and on Gatsplaas, Prince Albert, a skull of *Struthiocephalus* and some *Dicynodon* skulls. Mr. J. J. Hugo of Vanaswegensfontein, Loxton, also sent in some teeth of probably *Struthiocephalus*, from what was up to that date the furthest north-easterly site recorded in the *Tapinocephalus* zone.

In 1953 Toerien published an important paper in which a basis for the classification of the anomodonts is presented. All the known forms from the *Tapinocephalus* zone are considered and the following new forms described: *Brachyuraniscus merwevillensis* from Buffelsvlei collected by the C. J. van der Horst Expedition in 1945, *Broilius antjiesfonteinensis* collected by Kitching in 1946 on Antjiesfontein, *Dicynodon vanderhorsti* from Antjiesfontein, also found by Kitching, as also *Dicynodon antjiesfonteinensis* and *Dicynodon schroederi*, collected

by Kitching on Klein-Waterval.

In the same year Boonstra attempted to bring the known titanosuchians into taxonomic order and published a photograph of a life-sized reconstruction of the head of *Anteosaurus*. He also published two photographs of the life-sized reconstruction of *Hipposaurus* and an account of the cranial morphology of *Struthiocephalus* with a life-sized reconstruction of the head, and finally in this year discussed the articulatory region in some pristerognathids and proposed the following new forms: *Theriodes cyniscus*, *Pristerognathus roggeveldensis*, *Maraisaurus parvus* and *Alopecognathus angusticeps*.

In a lecture on Gondwanaland during 1953 Haughton discussed the *Tapinocephalus* zone and its fauna. In this year the owner of the farm Sandrivier, R. L. Jack, found part of the skull of a *Tapinocephalus atherstonei*.

In 1954 Boonstra studied the pristerognathids in the South African Museum and described the following new forms: *Scymnosaurus major*, *Ptomalestes avidus*, *Pristerosaurus microdon*, *Cynariognathus paucioridens*, the new generic name *Pristerognathoides* for *Alopecognathus minor*, and *Pristerognathus roggeveldensis* and *Pristerognathus vanwyki*, and erected a new species *Pristerognathoides parvus*.

In a study of the genus *Anteosaurus* Boonstra (1954*a*) named the following new forms: *A. acutirostris*, *A. crassifrons*, *A. major*, *A. laticeps*, *A. cruentus*, *A. levops*, *A. minusculus* and later also *Micranteosaurus parvus* and *Paranteosaurus primus*, and for *Anteosaurus minor* the new generic name *Pseudonteosaurus*.

In February, 1954, Boonstra made a skull, collected by Cairncross in 1918 near Prince Albert Road, the type of a new species of scaloposaurid, under the name *Blattoidealestes gracilis*.

In January, 1955, Boonstra described a specimen, collected by Haughton in 1916 on Abrahamskraal, under the name *Struthiocephalellus parvus*. In a detailed comparative account of the girdles and limbs of the South African Dinocephalia Boonstra also proposed the following new names for new forms: *Scapanodon septemfontis*, *Parascapanodon avifontis*, *Jonkeria koupensis*, *Jonkeria parva* and *Jonkeria rossouwi* and divided the South African Dinocephalia into four infra-orders, viz. Tapinocephalia, Titanosuchia, Anteosauria and Styracocephalia.

In 1955, in his book *Evolution of the vertebrates*, Colbert suggested the splitting up of the Dinocephalia, thus anticipating Watson & Romer (1956). Colbert published only one figure of the dinocephalian skull, and this of the inadequately known *Delphinognathus*, and quite erroneously shows a fossa between jugal and quadratojugal.

In 1956 Watson & Romer, in their classification of the therapsids, split the sub-order Dinocephalia – placing the infra-order Titanosuchia composed of the Brithopodidae, Anteosauridae and Jonkeriidae in the sub-order Theriodontia and the infra-order Dinocephalia (Tapinocephalia) composed of the Deuterosauridae, Moschopidae and Tapinocephalidae in the sub-order Anomodontia.

This arrangement is followed by Romer in his *Osteology of the reptiles*, but

Von Huene in his textbook retains the Unterordnung Dinocephalia with a Famielienkreis Tapinocephaloidae (Moschopidae, Struthiocephalidae, Tapinocephalidae) and a Familienkreis: Titanosuchoidea (Deuterosauridae, Brithopodidae, Titanosuchidae, Jonkeriidae) and a Familienkreis Burnetiamorpha consisting of *Styracocephalus* and *Burnetia*.

Kermack in 1956 studied the tooth replacement in some therocephalians from this zone housed in the British Museum.

Boonstra and Zinn collected eight Therocephalia, eight Pareiasauria, 20 Dinocephalia, four Anomodontia, one amphibian and two fishes on a trip in the *Tapinocephalus* zone.

Also in 1956 Boonstra published figures of skulls of *Tapinocephalus*, *Phocosaurus*, *Mormosaurus* and *Keratocephalus* and a photograph of a life-sized reconstruction of *Bradysaurus seeleyi* exhibited in the South African Museum.

During 1957 Boonstra and Zinn undertook four short collecting trips in the *Tapinocephalus* zone obtaining 24 pareiasaurian, 61 dinocephalian, 14 therocephalian and three anomodont specimens. On one of the trips S. Fourie, post-graduate student of Stellenbosch (later palaeontologist at the National Museum in Bloemfontein), was taken along.

In the same year Boonstra established the new species *Moschops koupensis* and figured other moschopids in the museum collection and showed that in *Delphinognathus* there is no lateral foramen but a notch between jugal and quadratojugal.

In 1958 Brink described a good skull of *Struthiocephalus kitchingi*.

During 1959 Boonstra, with Zinn, C. Gow and R. Rau as assistants, during two trips in the Koup collected two pareiasaurs, 71 therocephalians, 381 anomodonts, 41 dinocephalians (including seven rather poor specimens of *Styracocephalus* of which hitherto only the unique type specimen was known), three stegocephalians, one *Eunotosaurus* and four gorgonopsians.

In 1960 three collecting trips were undertaken by Boonstra and Zinn, with Gow and H. Boonstra accompanying them on one trip each. The haul consisted of 31 dinocephalians, 21 therocephalians, 92 anomodonts, 11 pareiasaurs, one stegocephalian and a fairly good skull of the rare *Hipposaurus*.

During 1961 Boonstra had the opportunity of visiting Moscow where he studied all the Russian material related to the *Tapinocephalus* zone forms of South Africa.

In 1962 Boonstra published a paper on the dentition of the titanosuchian dinocephalians and showed that these forms, although retaining a canine, were really herbivores.

In the same year Boonstra and Zinn explored both the southern and northern outcrops of the zone east of longitude 22° 35′ and found the exposures poor in the southern part but good in the north, but both areas yielded only a couple of scraps. It would thus appear that the fauna of those times were concentrated in the area to the west of this line.

In 1963 Boonstra in his paper 'Early dichotomies in the therapsids',

including data obtained during his Russian visit, emphasized the fact that the therapsid fauna of the *Tapinocephalus* zone was already greatly diversified and that the main branches must have arisen in Ecca times. In a further paper, 'Diversity within the South African Dinocephalia', the relationships of the four families (Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracocephalidae) were stressed as also the herbivorous habit of the Titanosuchidae. It was also suggested that the various species of *Struthiocephalus* represented growth stages of a single species.

Since 1964 Boonstra has published a series of studies on the girdles and limbs of the early Therapsida and also an account of a very well preserved skull of *Struthiocephalus*, where the relations of the stapes could be determined. The studies on the locomotor apparatus of the early therapsids were concluded in 1967 with a paper entitled 'An early stage in the evolution of the mammalian quadrupedal walking gait'.

In 1967 a paper appeared by Cys based on a therocephalian specimen collected by Camp.

In 1968 Boonstra published a paper on the basicranial axis of the Dinocephalia based on serial cross-sections cut by circular diamond-studded saws.

In the same year Boonstra also published a paper, 'The terrestrial reptile fauna of *Tapinocephalus* zone age and Gondwanaland'.

The Fauna as a Whole

Since Owen in 1876 described the first specimen from the *Tapinocephalus* zone under the name *Tapinocephalus atherstonei*, 152 species of reptiles have been named from this zone in South Africa by 15 authors.

The number of specimens collected from this zone is only very approximately known. I have not been able to obtain accurate lists from the various institutions, in South Africa as well as overseas, which house such collections. The South African Museum houses the largest collection, viz. 1,553 specimens. The other South African institutions together house approximately 77 of which the Bernard Price Institute has 58. In overseas institutions there must be over 400 specimens; in London there are at least 104, in Chicago 93, in New York 41 and an unknown number in Washington, California, Munich, Berlin and Vienna. It is thus very probable that well over 2,000 specimens have been collected from this zone.

To indicate the relative occurrence of the various groups of reptiles I give here a table of the number of specimens in each group in the collection of the South African Museum:

Dicynodontia	705
Therocephalia	422
Dinocephalia	439
Pareiasauria	160
Gorgonopsia	22
Eunotosauria	5

All the known specimens from this zone in South Africa come from the western part of the main Karoo Basin, lying approximately between longitudes 20° to 23° and latitudes 31° 20′ to 33°. The area concerned cannot be more than about 20,000 sq. miles, which gives a yield of about 1 specimen per 10 sq. miles. The Koup, lying between the Nuweveldberge and the Swartberg, has yielded well over 90% of the specimens. The rest come from the Moordenaar's Karoo and a strip of the Nuweveld stretching from the Klein Roggeveld eastwards through the towns of Sutherland, Fraserburg and Loxton.

It is not known with certainty whether rocks of this zone extend north-eastwards into that part of the main Karoo Basin which extends into the Transvaal and Natal to form a narrow outcropping belt between the underlying Ecca beds and the overlying higher zones of the Karoo beds. If so, the basin in which the sediments of *Tapinocephalus* zone times were deposited would be very large indeed, but on the inadequate facts I believe that the zone wedges out. The present extensive drilling could supply the much needed stratigraphic data as a compensatory by-product if the search for oil in the Karoo beds proves unsuccessful, as I believe it will. At present we do know that the zone crops out east of longitude 23° as two belts lying respectively north and south of a westward tongue of younger Beaufort beds.

I have undertaken collecting trips eastwards along both these belts of outcrops; in the south as far as King William's Town and in the north as far as Deelfontein and found some scraps of bone. In the northern belt good exposures are present, but the southern belt is affected by the Cape Foldings and the beds lie at steep angles. This, together with the nature of the vegetation, reduces the extent of the exposures for collecting purposes, but even so some identifiable specimens would have been found if present in the numbers known from the western part of the basin.

We thus have to conclude that during *Tapinocephalus* zone times only the western part of the Karoo Basin was populated by a reptilian fauna living under conditions in which entombment was possible.

It is thus evident that without the help of the geological cartographer the palaeontologist has to work at a serious disadvantage. Only parts of the southern limits of the *Tapinocephalus* zone have been accurately mapped by our Geological Survey, but this institution, whose function it is, could very easily map the rest of the *Ecca–Tapinocephalus* zone boundary, although some other lithological criterium would have to be used for the northern boundary where the zone has a facies different to that in the south. Nowhere has the boundary between the *Tapinocephalus* and *Endothiodon* zones been accurately mapped. The Geological Survey has, moreover, done little to determine the conditions under which the sediments of this zone have been formed. Differences in the nature of the deposition from west to north-eastwards may very well account for the lack of entombment if in fact the fauna extended thus far. Only for the Merweville sheet – 198 – have adequate details of the nature of the zone been given and in the Skoorsteenberg – 166, Gamkapoort – 3321B, Prince Albert – 3322

and Grahamstown – 136 sheets less full details have been given. Here, Rossouw & De Villiers have found it possible to establish a threefold subdivision on lithological grounds and this has been a great help to the palaeontologists studying this fauna. If only we could get the contiguous areas of the zone mapped in this manner!

In the type area the *Tapinocephalus* zone is from six to seven thousand feet in thickness and consists of a succession of sandstones and mudstones with bands of chert and bands and lenses and nodules of calcareous and marly rocks. These are not continuous but wedge out laterally in irregular series of overlapping lenses. For a more detailed account of the lithology I refer you to the work of Rossouw, De Villiers and their colleagues. Here it will suffice to state that the beds were laid down in a fairly warm, rainy climate over a fairly level flood plain area, with periodic flooding and the formation of lakes, marshes and shallow pans or vleis which silted up with the inclusion of the bones of the reptiles living in or around these water patches.

Little is preserved of the flora in the form of leaves but fossil (silicified) wood is fairly abundant. There must, however, have been a well-developed *Glossopteris* flora considering the large number of herbivores in the fauna, but here again it is evident that plants and bones seldom tend to be preserved in the same beds. It has been suggested that the Ph values of the sediments have a bearing on this phenomenon.

An account of the nature of the preservation of the remains of the different groups constituting the fauna will be of interest in showing the nature of some of the ecological conditions prevailing at this time.

The pareiasaurs are mostly found in blue mudstone as complete skeletons, whose position indicates that the animals were entombed standing on their legs with the head held high as if they were trapped in soft mud. The skeletons occur singly and there is no suggestion of general catastrophes, but rather of individual non-violent deaths. With the number of carnivores present in the fauna the presence of so few disarticulated pareiasaur skeletons is remarkable. Only once have I encountered the remains of a really juvenile animal and this was disarticulated. A number of half-grown skeletons are known, but most are mature.

In the case of the Dinocephalia, I know of only one skeleton (that of *Struthiocephalus whaitsi*) entombed in the usual pareiasaur condition. In both the tapinocephalids and the titanosuchids (both herbivorous groups) the skeletons after death apparently lay exposed on higher ground with the bones becoming widely scattered and then finally embedded in near-by depressions, filling up with argillaceous or arenaceous sediments, mostly as individual disarticulated bones, usually of the same animal. But at a number of places a thin bed has produced over a fairly small area a mass of bones of a number of separate individuals, e.g. bones of *Moschops* at Spitskop and at Kruisvlei, *Struthiocephalus* at Skoenmaker, *Criocephalus* at Moddergat and a number of struthiocephalines at Die Krans. At Kruisvlei the large number of bones of

Moschops was associated with a skull and some limb-bones of an anteosaurid. Of the anteosaurids, which were slinking carnivores, it is remarkable how few of the postcranial bones have been preserved, in contrast to the many large skulls.

It would appear that one has to postulate the presence of carrion eaters in addition to flowing water to account for the scattering and subsequent loss through over-exposure and decomposition of the postcranial parts. There was, of course, no hyaena-like destruction of the bones.

Of the Therocephalia from the *Tapinocephalus* zone I know of only one skeleton which lay practically complete on its 'belly'. This is an *Alopecognathus* from Lammerkraal. Otherwise the finds have been of isolated skulls or partly or wholly disarticulated postcranial parts of separate individuals. But at a number of places fairly thin lenticular beds, that had been formed in shallow depressions, have produced disarticulated remains of a number of individuals of the same or of different species. These have usually been associated with parts of small dicynodont forms.

The gorgonopsians are rare in this zone and the finds have been mostly of isolated skulls, but the type specimen of *Hipposaurus boonstrai* consisted of a neatly curled up complete skeleton overlain by a second skull.

Of the Dicynodontia a find at Mechau's Request consisted of a number of complete and partial skeletons in an arenaceous layer of about one foot in thickness. The indications here are that we have to postulate the occurrence of a local catastrophe. Isolated skulls occur throughout the zone, but by far the greater number of dicynodont specimens have been found in widely separate patches where the remains, also mainly skulls, have been eroded out of thin lenses, these lenses having been formed in shallow pans into which the disarticulated skeletal parts from higher ground had been transported by water. Often therocephalian remains are mixed up with the dicynodont material.

Although patches of initially soft mud surfaces, now indicated by the presence of ripple marks in the consolidated rock, are not uncommon, not a single track of any of the various groups of reptiles composing the fauna has as yet been encountered in the whole of this zone.

The geographical distribution of the collected specimens in the type Koup area shows some peculiarities, which are however readily accounted for. The collector soon thinks of the fossil-bearing part of the Koup as divided into two distinct areas, viz. a south-eastern and a north-western, with the railway line roughly forming the dividing line.

Because of the proximity of Cape Foldings, the beds of the overlying *Tapinocephalus* zone along the southern part of the area lie tilted, sometimes at considerable angles. The beds are thus seen in section, with the result that the likelihood of finding specimens is much smaller than it is in the northern part where the beds lie nearly horizontally.

The presence of monoclinal folds tends to bring the lower levels of the zone to the surface as one proceeds northwards. This applies specially to the

western part but less to the eastern part because the monoclines peter out eastwards. The north-western part of the Koup thus has more of the lower subdivisions exposed and these at low angles.

One would thus expect more specimens to have been collected from the lower division of the zone, but the collection in the South African Museum gives a contrary picture, viz. 555 specimens from the lower division and 769 from the upper divisions. (These numbers refer only to specimens whose stratigraphical position is known with certainty.)

The expected condition prevails as far as the Dinocephalia and Pareiasauria, large animals whose remains are mostly found singly, are concerned, viz. 362 low and 89 high.

It is the Therocephalia and Dicynodontia that cause the contradiction. The relation of the numbers of these two groups in the two horizons is, for the

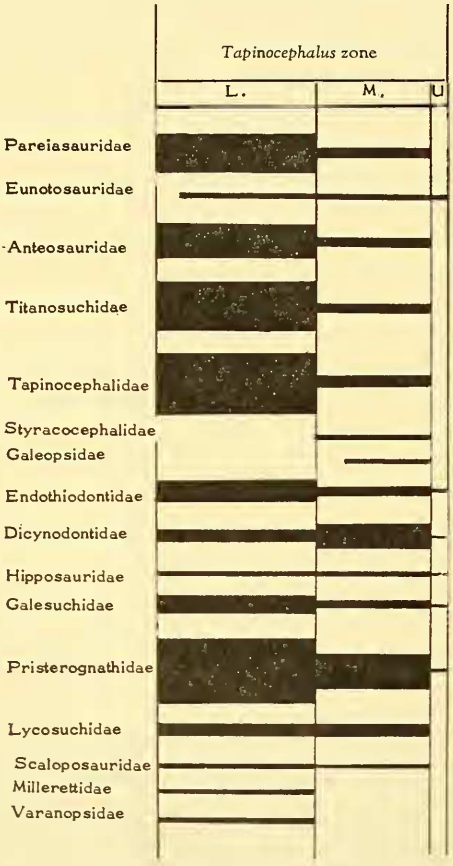

Fig. 1. Diagram to illustrate the relative numbers of the described species of the various reptilian families recorded from the *Tapinocephalus* zone.

former 99 : 119 and for the latter group 102 : 567. The reason for this is that in these two groups the mostly small skulls and snouts more often occur in patches with a great concentration of specimens in the higher divisions, where they are eroded out of lenses 4–5 inches in thickness, apparently formed in shallow pans into which the skeletal remains have been carried by flood waters. Such patches of greater concentration are rare in the lower division, and only a few are known, e.g. one on the farm Kleinkoedoeskop. If we plot the number of described species in the various families that constitute the fauna as they occur in the three subdivisions of the zone we get a graphical picture of the taxonomic composition of the fauna (fig. 1).

In the Dicynodontidae there are more species present in the middle division than in the lower division.

In the Eunotosauridae, Hipposauridae, Lycosuchidae and Scaloposauridae the lower and middle divisions have about the same number of species.

The Millerettidae and Varanopsidae occur only in the lower division, whereas the Styracocephalidae and Galeopsidae are not known from the lower division.

All the other families (Pareiasauridae, Anteosauridae, Titanosuchidae, Tapinocephalidae, Endothiodontidae, Galesuchidae and Pristerognathidae) are more abundantly represented in the lower division.

The upper division of the zone is very poorly stocked.

It is manifest that the reptile fauna is preponderantly therapsid. The pelycosaurs are represented by one advanced family—the Varanopsidae. There is one primitive Chelonian? family and the cotylosaurs are well represented by an advanced family—Pareiasauridae. The sauropsids are poorly represented by a single specimen of *Broomia perplexa*.

If we plot (fig. 2) the number of specimens in the South African Museum collection in the various infra-orders as derived from the three subdivisions we can readily see that the herbivores are represented in the lower division by nearly equal numbers of pareiasaurs, titanosuchians, tapinocephalians and Dicynodontia. In the middle division the former three groups are again about equally represented but in greatly reduced numbers, whereas the Dicynodontia are now very abundant.

The carnivores are represented by three groups—the Anteosauria, Gorgonopsia and Therocephalia, with the latter predominant, especially in the middle division.

In figure 3 I have plotted, not the number of specimens, but the number of described species in the three categories—herbivores, carnivores and insectivores. This tends to show that using the number of specimens rather than the number of species gives a truer picture especially as far as the middle division of the zone is concerned. For the zone as a whole, the fauna consists of 53% herbivores if one takes the number of recorded species as basis, but according to the number of specimens this figure is 80%, which is ecologically a better proportion.

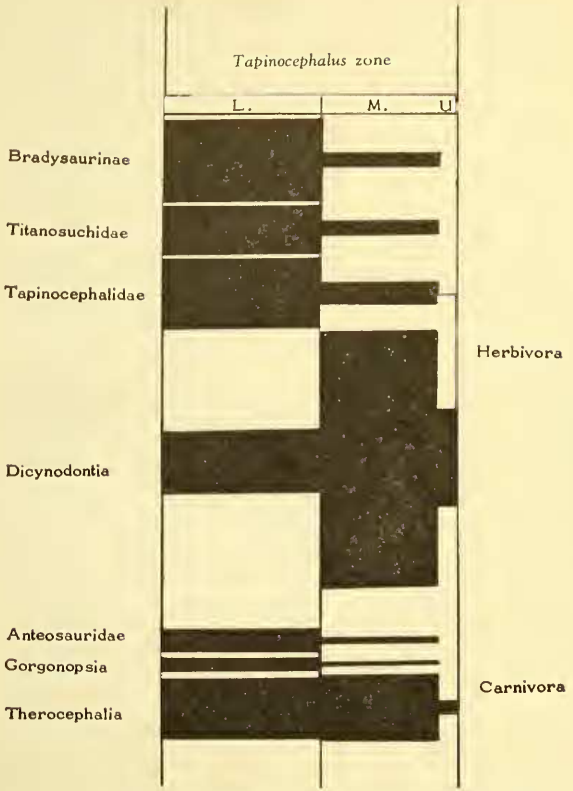

Fig. 2. Diagram to illustrate the relative numbers of the various herbivorous and carnivorous groups of reptiles during *Tapinocephalus* zone times. Based on the numbers of specimens in the collection of the South African Museum.

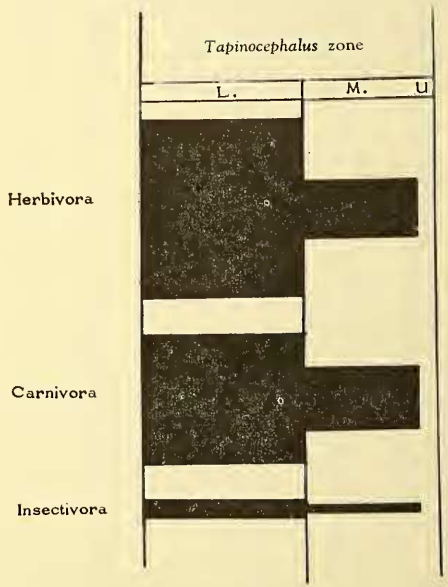

Fig. 3. Diagram to illustrate the relative occurcence of the total numbers of herbivores, carnivores and insectivores. Based on the numbers of the described species.

The present day mammalian fauna of South Africa, as recorded by Ellerman, gives the percentage of herbivores as 46% according to the number of species and 61% if the calculation is based on the number of genera.

This mammalian fauna consists of 125 genera and 221 species and the reptilian fauna of the *Tapinocephalus* zone has recorded 96 genera and 152 species.

The Non-reptilian Elements in the Fauna and the Flora

It is clear that what we know of the fauna of this zone gives a picture very far from reality.

One cannot believe that the four genera of Mollusca (*Carbonicola*, *Kidodia*, *Palaeomutela* and *Palaeanodonta*) were the sole representatives of the Invertebrata living at this time, but one can only speculate as to what teeming numbers of these soft-bodied animals were the contemporaries of the dominant reptiles.

Of the fish inhabiting the ponds, lakes and streams, only very few and poor specimens of palaeoniscids are known.

Even the Amphibia are poorly represented by a few specimens of the family Rhinesuchidae.

Of the plants, which must have constituted a fairly rich flora in order to have been able to nourish the numerous herbivorous reptiles, some more than a ton in weight, there is preserved some fossil wood of the genus *Dadoxylon*, and here and there some leaves of *Glossopteris*, *Schizoneura* and *Phyllotheca*.

Petroleum in the Rocks of the *Tapinocephalus* Zone

There is no evidence that the organic remains of the lowly animals we presume to have lived during these times on their demise provided the source of the hydrocarbons necessary for the formation of petroleum. The pseudocoal filling veins at a number of places in this zone is a residual product of petroleum, but this has been shown to have infiltered from beds underlying the rocks of the *Tapinocephalus* zone. The nature of these veins of pseudocoal clearly shows that they were unsuited as reservoirs for petroleum. It has, moreover, been shown that the texture and the structure of the rocks of this zone contra-indicate the possibility of the existence of other reservoirs for petroleum which may have arisen in adjoining beds (Rossouw, 1957).

Taxonomic Revision

Pareiasauridae

In 1929 Haughton & Boonstra attempted a classification of the then known pareiasaurs. As basis the structure of the teeth was considered. To avoid the pitfalls presented by postmortem deformations the proportions of the skull table, which would be least affected, were used, together with other features as a criterion for further diagnosis. On these bases eight genera were recognized in the fauna of the *Tapinocephalus* zone, viz. *Bradysaurus*, *Bradysuchus*,

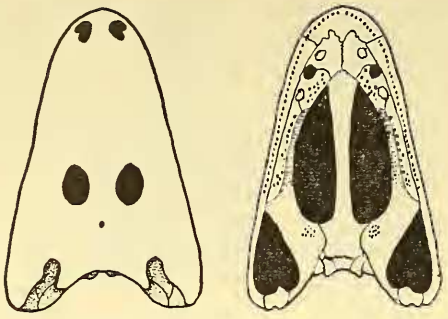

Fig. 4. Rhinesuchidae represented by *Rhinesuchus*. Skull in dorsal and ventral view.

Nochelesaurus, *Dolichopareia*, *Koalemasaurus*, *Brachypareia*, *Platyoropha* and *Embrithosaurus*. Subsequently I realized that *Platyoropha* was indistinguishable from *Bradysaurus*, and that *Bradysuchus*, founded on a feature recorded by Broom, which is pathological, is also a synonym of *Bradysaurus*.

Now with more material available and a reassessment of the effects of deformation on both the cranial and the postcranial skeleton, as well as such factors as sexual dimorphism, and age, and the recent stratigraphical subdivision of the zone a further reappraisement is suggested.

The genus *Embrithosaurus* stands on the basis of teeth with nine cusps arranged in three groups of three. So also does *Bradysaurus*, with less than nine cusps consisting of a terminal group of three cusps, an anterior group varying from 1–3 and a posterior group of 2–3 cusps. All the other genera have a cusp arrangement, with only slight variations, similar to that of *Bradysaurus* and can be included in this genus. Moreover, the genus *Brachypareia* appears to have been based on specimens which may very well be considered to be immature. Discounting the features liable to deformation the other noted differences can at most be specific. The genus *Bradysaurus* could then include the four species *baini*, *seeleyi*, *angusta* and *strubeni*.

At the time when our 'Pareiasaurian studies' were written the prevailing view was that the strata of the *Tapinocephalus* zone within the Koup, north of the Folded Belt, lay more or less horizontally. Consequently it was thought that the higher the altitude of the sites the higher was the level within the zone. On this basis it was found that a number of species lived unchanged from near the base to near the top of the zone. This was challenged by Broom, who maintained that it was unlikely that species could remain unchanged for this length of time, viz. according to Broom, 3–5 million years for the 1,900 ft thickness of the zone.

In 1952 Rossouw & De Villiers gave the thickness of the zone as 6–7,000 ft and were able to establish a threefold subdivision of the *Tapinocephalus* zone and, moreover, found that monoclinal folding brought the strata upwards as one proceeded from south to north, so that in the north where the surface

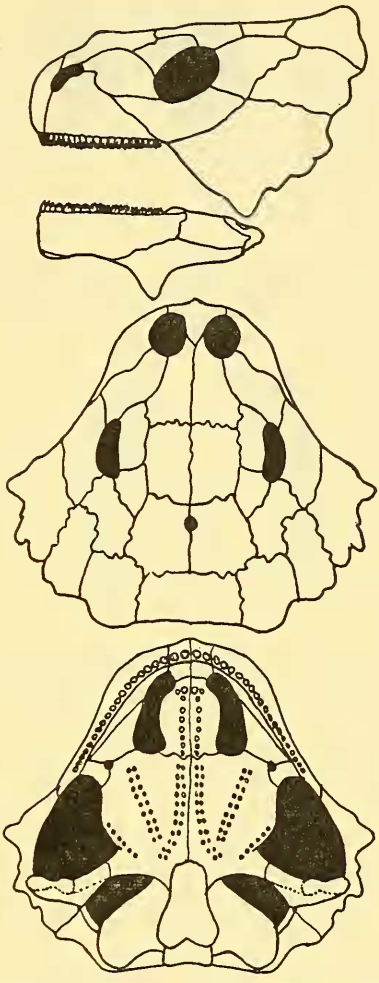

Fig. 5. Pareiasauridae represented by *Bradysaurus*. Skull in lateral, dorsal and ventral view.

altitude is the highest the lower subdivision becomes exposed on the surface. The stratigraphical level of all the fossil sites had thus to be determined anew.

Of the 70 specimens of pareiasaurs listed by Rossouw the distribution is as follows:

Upper subdivision	1?
Middle subdivision	8
Lower subdivision	61

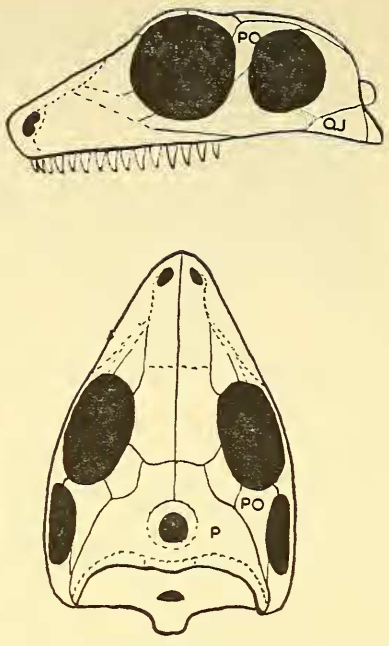

Fig. 6. Varanopsidae represented by *Anningia*. Skull in lateral and dorsal view.

The specimens entered into the South African Museum registers are distributed as follows:

Upper subdivision	0
Middle subdivision	17
Lower subdivision	128

There is some doubt as to whether the specimens listed above as from the middle part of the zone are correctly so placed. The localities are mostly defined as to the farm and some of these large farms have outcrops of both the lower and middle subdivisions exposed.

Both the genera *Bradysaurus* and *Embrithosaurus* are thus fully developed from near the base of the zone, with some stragglers possibly surviving into the middle part of the zone.

We have thus at least five species living unchanged through about 3,000 ft of strata. The time lap, according to Broom's figures would be:

$$\frac{3{,}000{,}000 - 5{,}000{,}000}{1} \times \frac{3000}{1900} \text{ years.}$$

As for myself I should not like to be implicated in this arithmetic exercise.

ANOMODONTIA

A suborder of therapsid reptiles. Without a coronoid process to the dentary. Quadrate large, anteriorly situated and supported by a strong quadrate ramus of the pterygoid. Carnivorous or herbivorous. It consists of the infra-orders Dinocephalia and Dicynodontia.

DINOCEPHALIA

An infra-order of anomodonts in which the pterygo-quadrate complex is greatly strengthened. Carnivorous or herbivorous. It contains in South Africa the families Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracocephalidae.

Anteosauridae

A family of dinocephalians which are fairly primitive carnivores, with long intermeshing incisors. A stage further advanced than the Russian Brithopidae.

From the *Tapinocephalus* zone seven genera have hitherto been named, viz. *Eccasaurus*, *Anteosaurus*, *Titanognathus*, *Dinosuchus*, *Micranteosaurus*, *Paranteosaurus* and *Pseudanteosaurus*.

Of these, *Dinosuchus* and *Titanognathus* have already been considered synonyms of *Anteosaurus* (Boonstra, 1954*a*).

Eccasaurus, with a holotype of which the cranial material consists of only a few typical anteosaurid incisors, appears to be only determinable as to family.

The skull fragment forming the holotype of *Pseudanteosaurus* can best be considered as an immature specimen of *Anteosaurus*.

Micranteosaurus, the holotype of which contains a small snout, has been considered a new genus only on account of its small size and I now propose that it be regarded as a young specimen of *Anteosaurus*.

ANTEOSAURUS

A genus of anteosaurids in which the postfrontal forms a boss of variable size overhanging the dorso-posterior border of the orbit.

We have 32 skulls of *Anteosaurus*, of which 16 are reasonably well preserved and on them ten species have been named. To differentiate between the species the following main characters have been used: the number, size and shape of the teeth, skull size, shape and the nature of the pachyostosis.

On re-examination it has become clear that the crowns of the teeth are seldom well preserved; basing the count for the dental formula on the preserved roots is unreliable as this is affected by age and tooth generation; size of skull is a function of age and also possibly sex; skull-shape is greatly affected by post-mortem deformation, and the variability in the pachyostosis, which may be specific in some respects, can just as well be the result of normal or morbid physiological processes. Specific diagnosis consisting of the enumera-

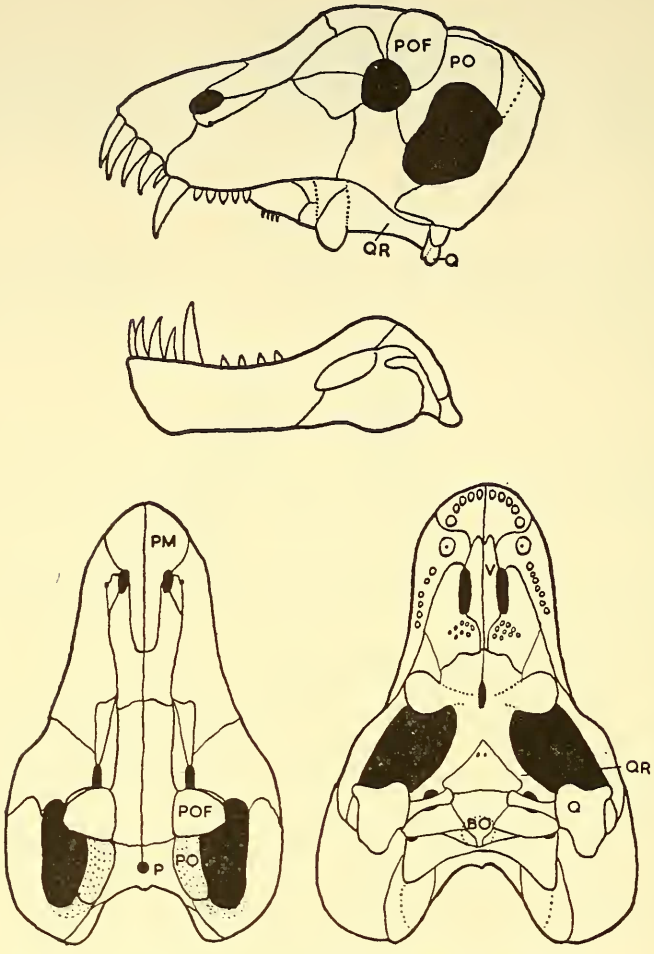

Fig. 7. Anteosauridae represented by *Anteosaurus*. Skull in lateral, dorsal and ventral view.

tion of differences of degree in features such as the above can hardly be considered as sufficient indication of the existence of discrete species.

I thus suggest that only the oldest trivial name be retained. *A. magnificus* thus has the following synonyms: *abeli*, *acutirostris*, *crassifrons*, *cruentus*, *laticeps*, *levops*, *lotzi*, *minor*, *minusculus*, *parvus*, *priscus* and *vorsteri*. Motivation for the synonymy can be given as follows: *cruentus*, *levops*, *minor*, *minusculus* and *parvus*, because the holotypes are immature animals; *lotzi* and *priscus* because the specimens are specifically indeterminable; *abeli*, *acutirostris*, *crassifrons*, *laticeps*, *major* and *vorsteri* because the characters used appear to be either the results of post-mortem deformation or, the degree of the pachyostosis and this as far as the pachyostosis is concerned, would fall within the range possible for individual variation and the age or sex.

PARANTEOSAURUS

A genus of anteosaurids in which the postfrontal is not developed to form a boss.

Titanosuchidae

These are fairly primitive herbivorous Dinocephalia in which the canine has been retained and the very strong incisors have a piercing talon and a crushing heel and the long series of postcanines have serrated spatulate crowns. There is very little pachyostosis. The family contains two groups, viz. the long-legged *Titanosuchus* and the short-legged species of *Jonkeria*.

When Owen described the first form in 1879 all the material from the Karoo was so obviously new to science that even the poorest specimen warranted description. *Titanosuchus ferox* was based on the roots of an incomplete set of teeth.

In the race to name as many new species as possible Broom added a ballast of names on just as poor material and even misidentified an obvious carnivorous anteosaurid skull as co-specific with the herbivorous *Titanosuchus ferox*.

Subsequently it has become apparent that even well-preserved batteries of teeth exhibit so much variation, even in the left and right sides of the same skull, that dental features are a very unreliable criterion for distinguishing between titanosuchids.

In total 24 names appear in the literature.

A critical evaluation of these names seriatim

1. *Titanosuchus ferox* Owen, 1879

The type material is such that a diagnosis based on the available features of the dentition is that given for the family which is based on the condition in *Jonkeria*. The associated limb-bones, however, enable us to formulate a generic diagnosis to distinguish this genus from *Jonkeria*.

2. *Titanosuchus cloetei* (Broom, 1903)

The characters determinable in this jaw-piece only allow one to determine the family.

3. *Scapanodon duplessisi* Broom, 1904

The cranial features are indeterminate. The humerus cannot be distinguished from that of *Titanosuchus* and *Scapanodon* thus becomes a synonym. The skull referred by Broom to the genus *Scapanodon* has been shown to fall within the limits set for the genus *Jonkeria*.

4. *Archaeosuchus cairncrossi* Broom, 1905

The type specimen is so poor that no diagnosis can be made. The specimen being indeterminable, the name is a *nomen dubium*.

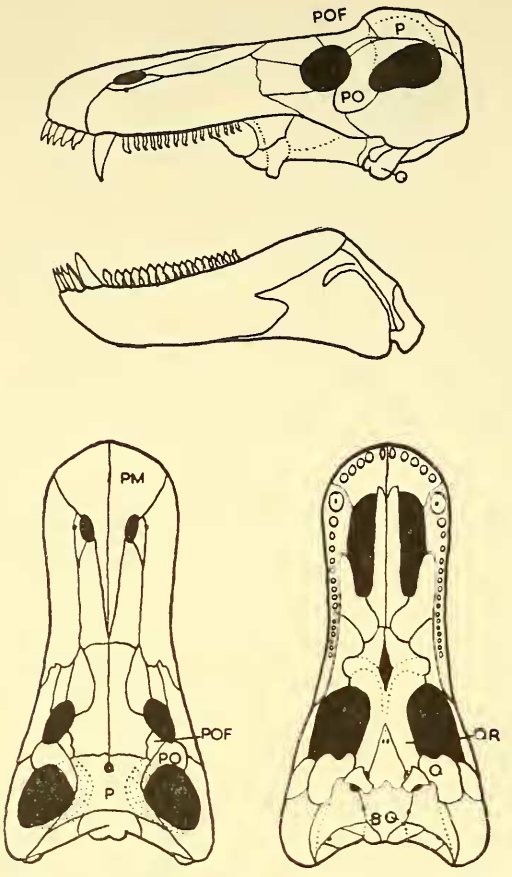

Fig. 8. Titanosuchidae represented by *Jonkeria*. Skull in lateral, dorsal and ventral view.

5. *Lamiasaurus newtoni* Watson, 1914

This jaw fragment cannot be identified even as to family—it may be either titanosuchid or anteosaurid.

6. *Titanosuchus dubius* (Haughton, 1915)

The teeth roots preserved only allow one to identify the specimen as being of the family Titanosuchidae.

7. *Jonkeria truculenta* Van Hoepen, 1916

Besides the good holotype, which consists of a good skull and much of the postcranial skeleton, there is another good skull with lower jaw known. In the South African Museum collection there are a number of specimens of which I have described the dentition. All these specimens show that the teeth are too variable for use in distinguishing between species of the genus. The genus *Jonkeria* is distinguishable from *Titanosuchus* on features of the limb-bones.

8. *Dinophoneus ingens* Broom, 1923

The holotype, together with its synonym, *Jonkeria pugnax*, and three other known skulls constitute a distinct species of *Jonkeria* as the genus is defined by me in 1953. The genera *Dinosphageus* and *Dinopolus* can also be included in the genus *Jonkeria*.

9. *Dinartamus vanderbyli* Broom, 1923

The fragments on which this name is based have features too indefinite for a generic diagnosis and can only be considered as titanosuchian indeterminate as to genus.

10. *Enobius strubeni* Broom, 1923

These pieces of jaw can only be identified as titanosuchian.

11. *Jonkeria vanderbyli* Broom, 1929

The holotype is a good skull of *Jonkeria* easily distinguishable from the other species of the genus.

12. *Dinosphageus haughtoni* Broom, 1929

This fairly good skull, with some limb-bones, shows no features that would exclude it from the genus *Jonkeria*, but can specifically be distinguished from the other species of the genus.

13. *Jonkeria crassus* Broom, 1929

In the holotype consisting of dentaries and postcranial bones, the humerus cannot be distinguished from that of *Jonkeria haughtoni*, and as there are no other distinctive features it should be considered a synonym of *J. haughtoni*.

14. *Phoneosuchus angusticeps* Broom, 1929

This good mandible has all the characters of the genus *Jonkeria* and I can find nothing to exclude it from the species *truculenta*.

15. *Jonkeria pugnax* Broom, 1929

I have already in 1935 shown this to be a synonym of *J. ingens*.

16. *Dinocynodon dubius* (Broom, 1929)

The oval outline of the cross section of the canine can hardly be a character so important as to justify a new generic name. It can only be identified as titanosuchian.

17. *Scullya gigas* Broom, 1929

This poorly preserved snout shows no definite titanosuchian characters. The possible presence of teeth on the palatine may be an anteosaurid character. The specimen must be considered indeterminable.

18. *Dinopolus atrox* Broom, 1936

The features exhibited in this snout are those known as characters of the genus *Jonkeria* and cannot be used for a specific diagnosis. *Dinopolus atrox* is thus an indeterminable species of the genus *Jonkeria*.

19. *Scapanodon septemfontis* Boonstra, 1955

Only postcranial bones are known. As the imperfect humerus cannot be distinguished from that of *Scapanodon duplessisi*, *septemfontis* represents a synonym of the former species and thus of the genus *Titanosuchus*.

20. *Parascapanodon avifontis* Boonstra, 1955

The humerus and femur are so similar to that of *Titanosuchus* and *Scapanodon* that this form should be included in the genus *Titanosuchus*.

A number of specimens, described by me under the name *Parascapanodon*, together give a full picture of the dentition, but nothing determined in these specimens is incompatible with the inadequately preserved dentition of the holotype of *Titanosuchus ferox*. I thus suggest that the characters—cranial, dental and postcranial—described under the names *Titanosuchus*, *Scapanodon* and *Parascapanodon* be considered as diagnostic of the form *Titanosuchus ferox*.

21. *Jonkeria koupensis* Boonstra, 1955

The holotype is a good pelvis readily distinguishable from that of any other known species of *Jonkeria*.

22. *Jonkeria parva* Boonstra, 1955

A small humerus is quite distinct from that of the other known species of *Jonkeria*.

23. *Jonkeria rossouwi* Boonstra, 1955

The holotype consists of postcranial bones readily distinguishable from those of the other species of the genus. Moreover, two other specimens are known that show the same distinctive features.

24. *Jonkeria boonstrai* Janensch, 1959

Janensch has given a convincing diagnosis of the specific features of the holotype skull. He also stresses the herbivorous nature of the dentition.

The family Titanosuchidae is thus composed of two genera and nine species. The genera *Titanosuchus* and *Jonkeria* cannot in the present state of our knowledge be distinguished from one another on either cranial or dental characters. But in *Titanosuchus* the limb-bones are long, whereas in all the species of *Jonkeria* they are short and squat.

In *Jonkeria* some of the species, where good cranial material is known, can be distinguished on differences in cranial structure and the others only on postcranial features.

Tapinocephalidae

This is an advanced family of herbivorous Dinocephalia without a 'canine'; all the teeth in maturity have a talon and a crushing heel and the upper and lower teeth of the whole battery intermesh. The pachyostosis is moderately to very greatly developed.

The family can be subdivided into a number of sub-families, viz. Struthiocephalinae, Tapinocephalinae, Moschopinae and Riebeeckosaurinae.

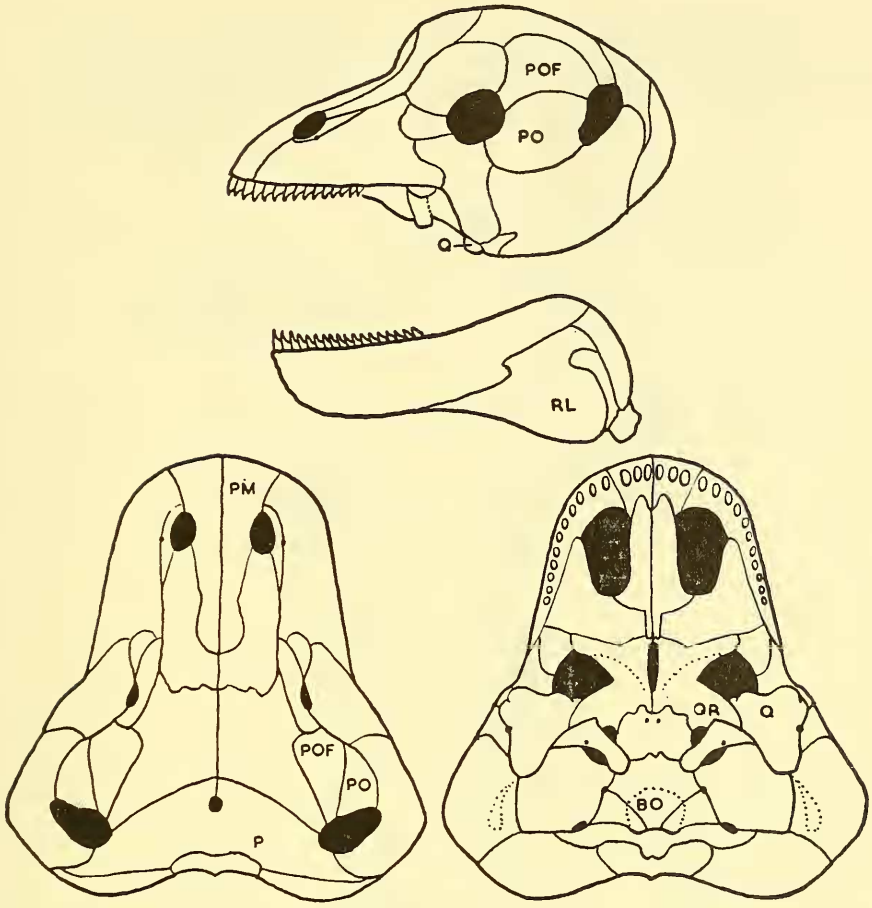

Fig. 9. Tapinocephalidae represented by *Tapinocephalus*. Skull in lateral, dorsal and ventral view.

Struthiocephalinae

These are tapinocephalids with a long fairly strong snout and with moderate pachyostosis. Six genera have been named. Two of these, *Struthiocephalellus* and *Moschosaurus*, appear to be growth stages of *Struthiocephalus* and are thus synonyms.

Struthiocephalus is a genus with a naso-frontal boss in maturity. The seven described species—*parvus*, *longiceps*, *milleri*, *whaitsi*, *rheederi*, *akraalensis* and *kitchingi*—have been shown by me to represent a growth series and six of these trivial names are thus synonyms of the first described species, viz. *whaitsi*.

Struthiocephaloides is a genus without a naso-frontal boss in maturity. The species *duplessisi* is wide across the tabulars whereas *cavifrons* is narrow across the tabulars.

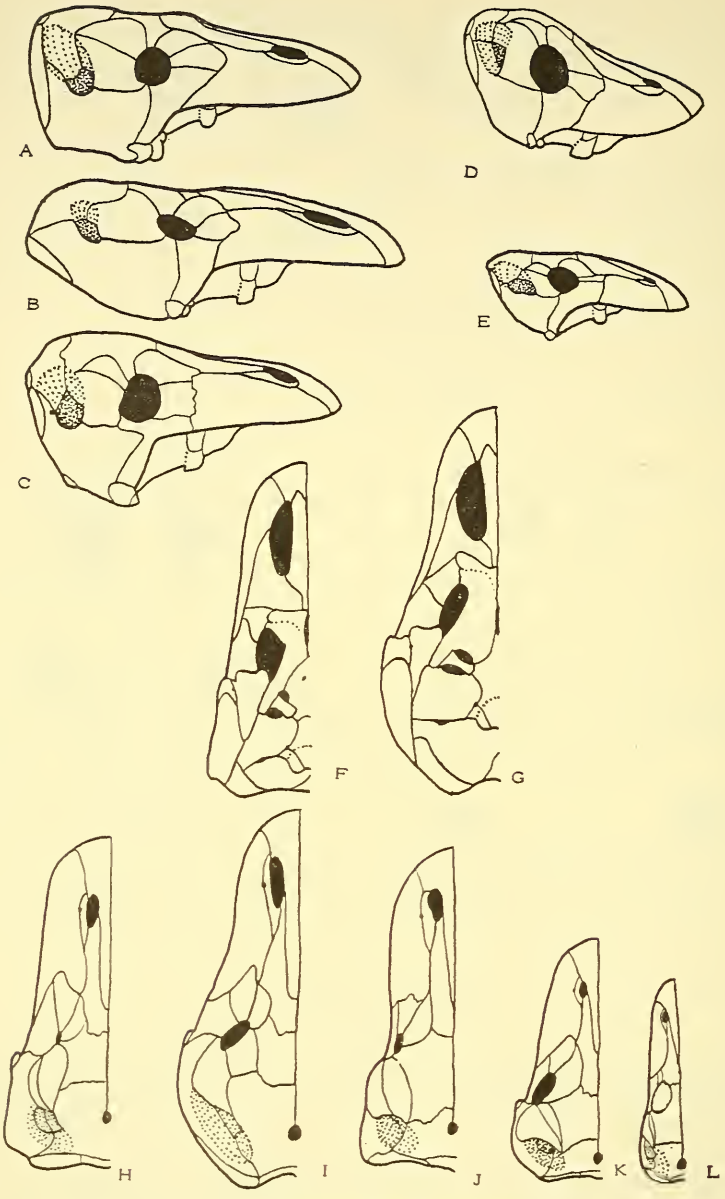

Fig. 10. Struthiocephalinae represented by:

A. *Struthiocephalus*
B. *Struthiocephaloides*
C. *Taurocephalus*
D. *Struthionops*
E. *Moschosaurus*

} Skulls in lateral view.

F. *Struthiocephalus*
G. *Struthiocephaloides*

} Skulls in ventral view.

H. *Struthiocephalus*
I. *Struthiocephaloides*
J. *Taurocephalus*
K. *Struthionops*
L. *Moschosaurus*

} Skulls in dorsal view.

Struthionops, with one species, *intermedius*, is a genus without a naso-frontal boss, with moderate pachyostosis and a snout only moderately long.

Taurocephalus, with one species, *lerouxi*, has a long and strong snout and with a long series of teeth – twenty in the upper jaw.

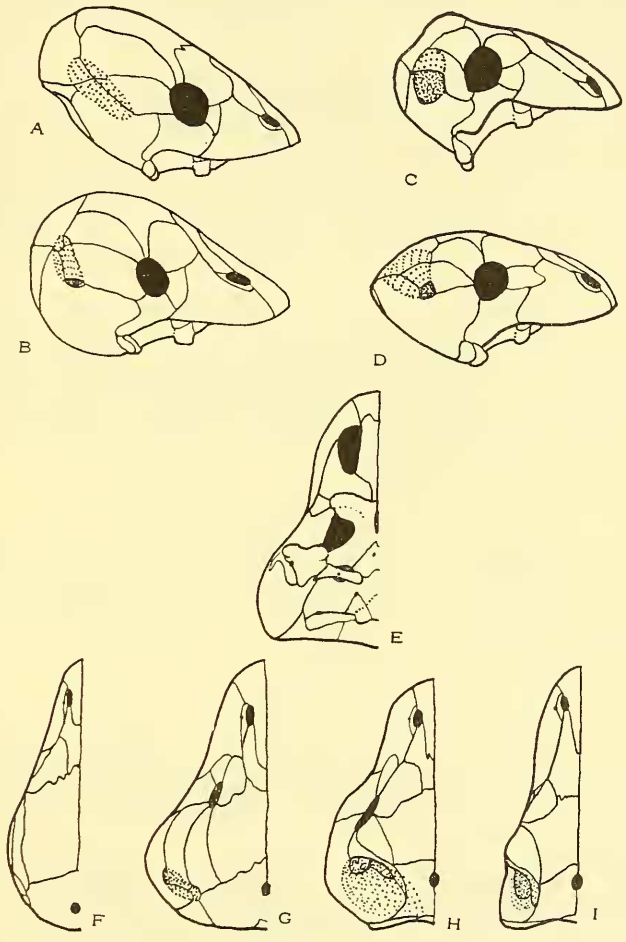

Fig. 11. Moschopinae represented by:

A. *Criocephalus*
B. *Moschops*
C. *Delphinognathus*
D. *Avenantia*
} Skulls in lateral view.

E. *Moschops* Skull in ventral view.

F. *Criocephalus*
G. *Moschops*
H. *Avenantia*
I. *Delphinognathus*
} Skulls in dorsal view.

Moschopinae

Medium-sized tapinocephalids with a short snout running up to the frons in an even curve. The cranial roof is moderately to very greatly thickened by pachyostosis.

Delphinognathus, a monotypic genus with species *conocephalus*, is known from a single skull which has a conical boss on the parietal surrounding the pineal foramen. There is a notch on the ventral edge between the jugal and quadratojugal. The pachyostosis is moderate. It may possibly be a young skull of a *Moschops* species.

Avenantia kruisvleiensis is only moderately pachyostosed and the intertemporal region is narrow and the temporal fossa large.

Moschops (with synonyms *Moschoides*, *Agnosaurus*, *Moschognathus* and *Pnigalion*) is a genus strongly pachyostosed with a broad intertemporal region and greatly reduced temporal fossae. There are two species—*capensis* and *koupensis*—known from good material, and two species—*whaitsi* and *oweni*—of doubtful validity.

Criocephalus: in addition to the poor holotype specimen a further half-dozen skulls are now known. In this genus the intertemporal region is very broad, overhanging the greatly reduced temporal fossae. The cranial roof is very greatly thickened by pachyostosis to make the parietal canal enormous. The species—*vanderbyli*—is South African and *gunyankaensis* is Rhodesian.

Riebeeckosaurinae

This is a subfamily of the tapinocephalids in which the only species, *Riebeeckosaurus longirostris*, known from two skulls, has a skull with a very long and slender snout and a narrow intertemporal region which forms a narrow sagittal crest. The pachyostosis is moderate.

Tapinocephalinae

The tapinocephalines are large and massive tapinocephalids in which the snout is moderate to short and weak; they have either a prominent naso-frontal boss or a greatly swollen frons. They are greatly to very greatly pachyostosed.

Of the described genera *Pelosuchus*, without cranial parts known, is, on the postcranial features, a synonym of *Keratocephalus* and the snout of *Taurops* is so similar to that of *Tapinocephalus* that it should be included in that genus. The greatly variable skulls known of the genera *Mormosaurus* and *Keratocephalus* form a link between the subfamilies Struthiocephalinae and Tapinocephalinae.

Tapinocephalus: the one species—*atherstonei*—is known from a number of skulls and postcranial bones. The skull is large with a massive swollen frons and a short weak snout. The skull roof is greatly pachyostotic.

Phocosaurus megischion differs from *Tapinocephalus* in that the transition from the frons to the snout is not abrupt.

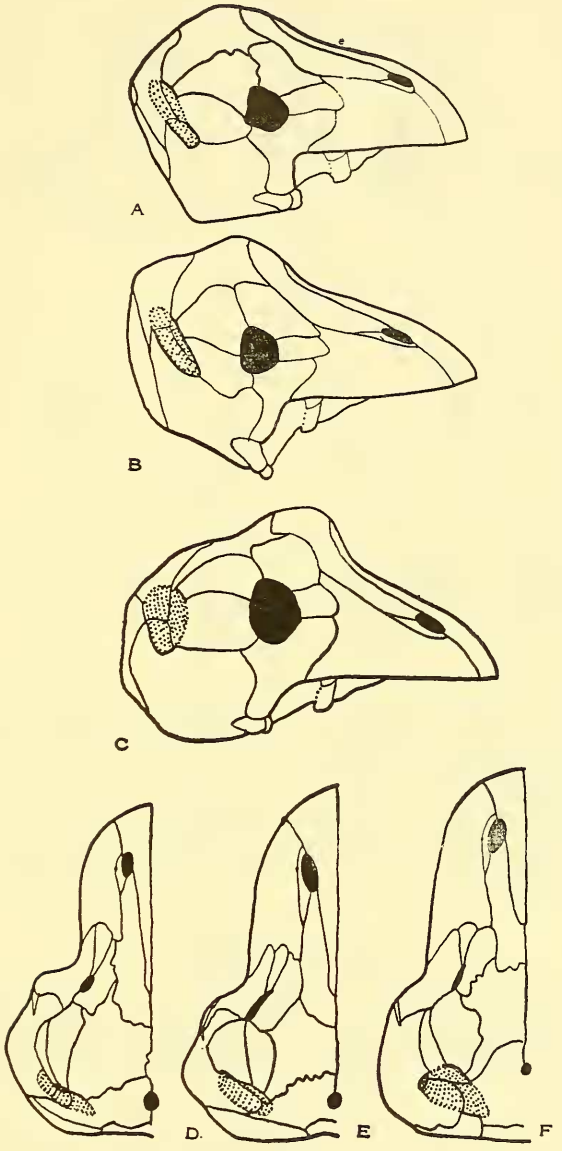

Fig. 12. Tapinocephalinae represented by:

A. *Phocosaurus*
B. *Mormosaurus* } Skulls in lateral view.
C. *Keratocephalus*
D. *Phocosaurus*
E. *Mormosaurus* } Skulls in dorsal view.
F. *Keratocephalus*

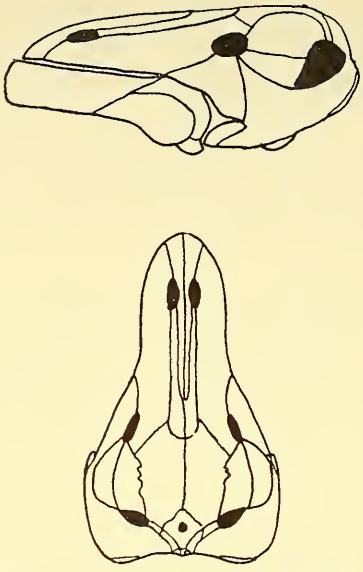

Fig. 13. Riebeeckosaurinae represented by skull of *Riebeeckosaurus* in lateral and dorsal view.

Mormosaurus: in the holotype skull of the species, *seeleyi*, there is a naso-frontal boss but in another skull there is a moderately strong frons. The snout is strong and the pachyostosis moderate.

Keratocephalus: a number of skulls described and referred to the type, *moloch*, show considerable variability in the pachyostotic development. There is a prominent naso-frontal boss and the strength of the snout varies considerably.

Styracocephalidae

In this family a number of imperfect skulls are known to constitute a family of small advanced herbivorous dinocephalians with the retention of a moderate canine. Characteristic are the prominent posteriorly directed tabular bosses.

DICYNODONTIA

In the *Tapinocephalus* zone the Dicynodontia are represented by small advanced anomodonts with edentulous beaks covered by horn and with the maxillary and dentary teeth greatly reduced or absent. They differ from the Dinocephalia in that, although the quadrate is strong, the quadrate ramus of the pterygoid is not greatly strengthened and by the characteristically horizontally turned squamosal bar.

Two families—Endothiodontidae and Dicynodontidae—occur in the *Tapinocephalus* zone.

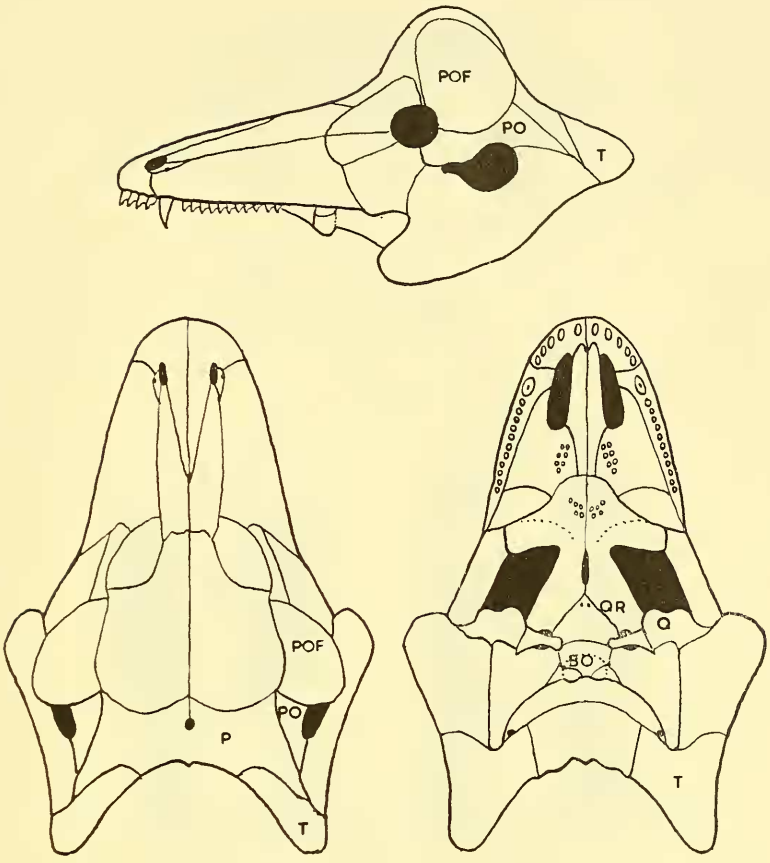

Fig. 14. Styracocephalidae represented by skull of *Styracocephalus* in lateral, dorsal and ventral view.

Endothiodontidae

A family of dicynodonts with postcanine (molar) teeth in the maxilla. Seven genera have been named of which two have been found to be synonyms, viz. *Opisthoctenodon* of *Pristerodon* and *Brachyprosopus* of *Brachyuraniscus*.

Brachyuraniscus is a genus with three species with pineal boss, in which the molars are in a row and the maxilla reaches the choana.

Broilius, with one species without pineal boss, in which the molars are irregularly spaced and the maxilla reaches the choana.

Koupia, with one species; the molars are irregularly spaced and the relations of the maxilla to the choanal border not determined.

Robertia broomiana: the molars are irregular, there is no pineal boss and the maxilla does not enter the anterior choanal border.

Pristerodon brachyops: the molars are in a row, without a pineal boss and the maxilla reaches the choana.

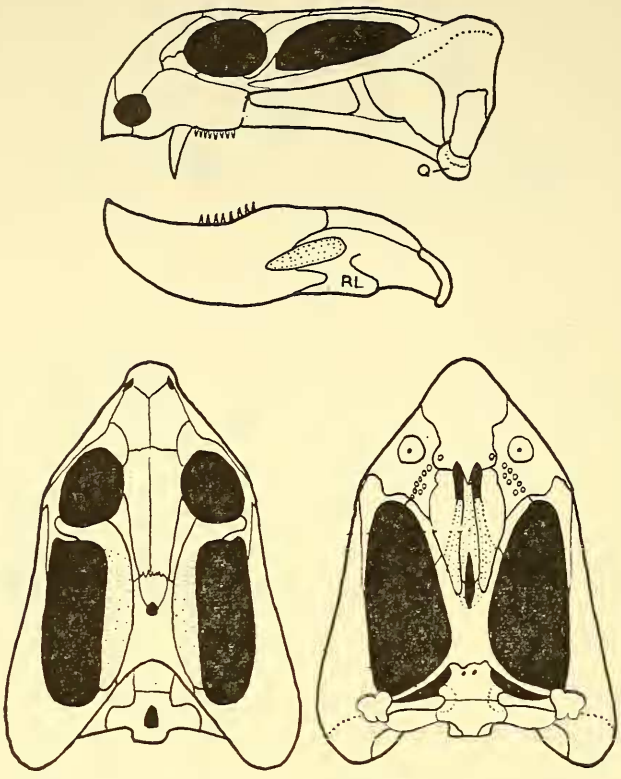

Fig. 15. Endothiodontidae represented by composite figures of the skull in lateral, dorsal and ventral view.

Dicynodontidae

A family which in the *Tapinocephalus* zone consists of two genera of small dicynodonts without postcanine (molar) teeth.

Dicynodon, with eight described species from this zone, in which the maxilla does not reach the choana.

Oudenodon, with one species, where the maxilla reaches the choanal border.

THERIODONTIA

A suborder of the Therapsida in which the South African forms have a coronoid process to the dentary; the quadrate has not moved anteriorly, it is small and the quadrate ramus of the pterygoid is weak. Carnivorous or insectivorous. In the *Tapinocephalus* zone the sub-order is represented by the two infra-orders Gorgonopsia and Therocephalia.

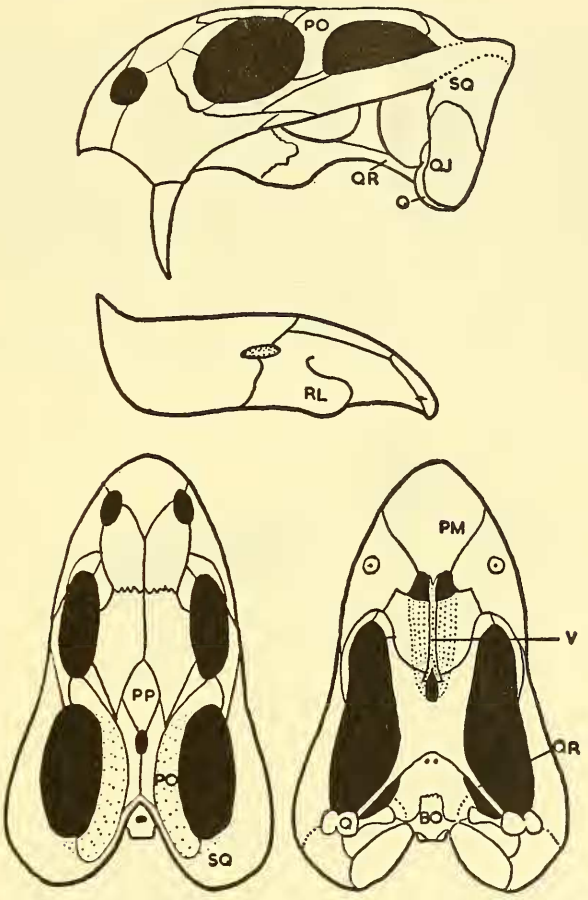

Fig. 16. Dicynodontidae represented by the skull of *Dicynodon* in lateral, dorsal and ventral view.

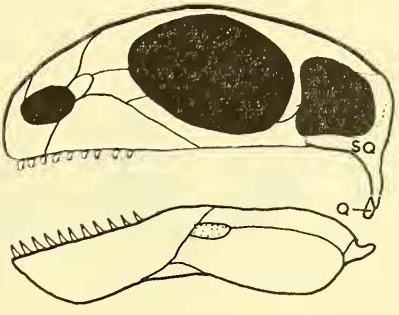

Fig. 17. Galeopsid represented by the skull of *Galepus* in lateral view.

GORGONOPSIA

This infra-order, as represented in the *Tapinocephalus* zone, consists of fairly primitive theriodonts, in which the intertemporal region is still very wide with the postorbital in its dorsal part lying horizontally, with the jaw adductors originating from the under surface of the parietal and postorbital.

Of the nine described genera I regard two (*Cyniscodon* and *Eriphostoma*) as without diagnosable generic characters and the two poor specimens as indeterminate gorgonopsians. Of the remaining seven a further two (*Aelurosauroides* and *Broomisaurus*) are represented only by snouts.

The described genera have been placed in five families by Watson & Romer (1956). I recognize only two, viz. Hipposauridae and Galesuchidae.

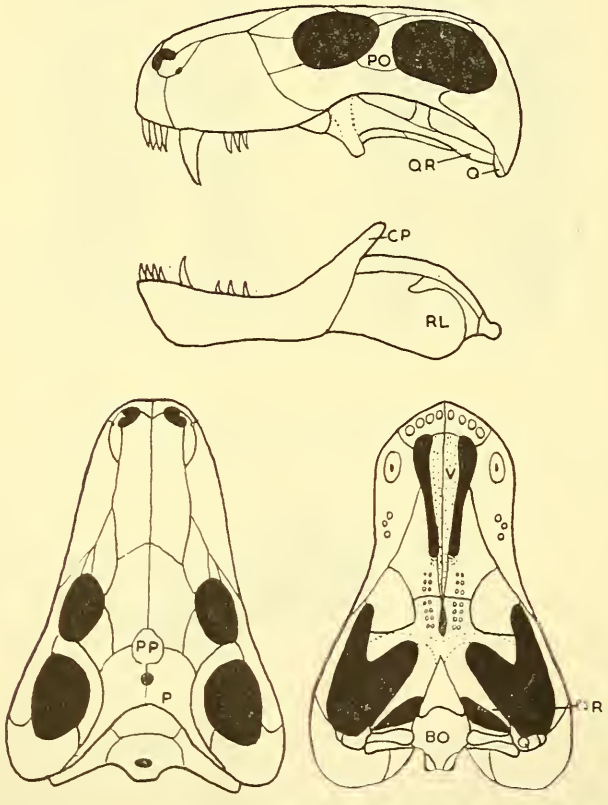

Fig. 18. Galesuchid gorgonopsian, composite figures based on the known genera. Skull in lateral, dorsal and ventral view.

Hipposauridae

The representatives of this family in the *Tapinocephalus* zone consist of three fairly good skulls and three partial skulls forming a single genus *Hipposaurus* with two species—*boonstrai* and *major*. These are primitive gorgonopsians only little advanced beyond the Russian Phthinosuchidae, which are the most primitive gorgonopsians known. The hipposaurids are characterized by a very broad intertemporal region, a long tooth row, a deep suspensorium and by the fact that the snout is curved down strongly in relation to the skull roof.

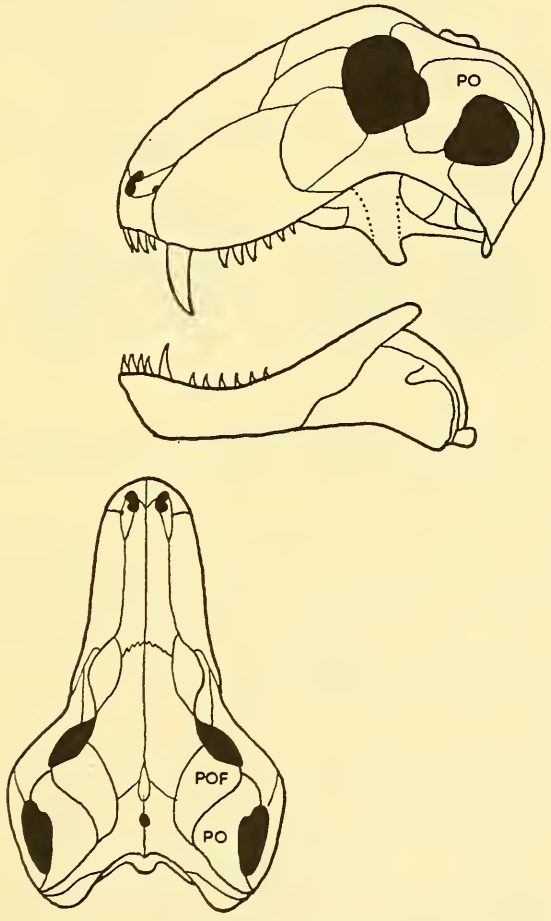

Fig. 19. Hipposaurid gorgonopsian represented by the skull of *Hipposaurus* in lateral and dorsal view.

Galesuchidae

Primitive gorgonopsians with a broad intertemporal region, a reduced postcanine series, a shallow suspensorium with the quadrate extending to just below the level of the alveolar border and the snout is not bent down.

Pachyrhinos has a fairly large skull, with a dental formula I5, C1, PC4.

The other genera are fairly small and appear fairly closely related.

Eoarctops has for the upper jaw a dental formula I4, C1, PC3.

Galesuchus has for the upper jaw a dental formula I?, C1, PC4.

Scylacognathus has for the upper jaw a dental formula I5, C1, PC5.

THEROCEPHALIA

This infra-order, as represented in the *Tapinocephalus* zone, consists of small to large primitive theriodonts in which the intertemporal region is narrowed with usually a sagittal crest and the posterior process of the post-orbital lies vertically so that the jaw adductors arise from the lateral face of the postorbital and parietal.

A large number of genera (24) have been described and these can be arranged in four families – Pristerognathidae, Lycosuchidae, Alopecodontidae and Scaloposauridae.

Pristerognathidae

Primitive Therocephalia with five to six incisors and a single canine and two to nine variable postcanines. The epipterygoid is narrow. Two subfamilies have been established – Scymnosaurinae and Pristerognathinae.

Scymnosaurinae

Fairly large to large pristerognathids with five incisors and two to six postcanines. Five genera with seven species have been assigned to this subfamily, which appears to be very variable.

Scymnosaurus, with three species, is known from six large but incomplete skulls. Postcanines fairly weak to medium varying in number – 2, 3 or 4.

Glanosuchus, with one species, is known from two good skulls and two snouts. Large, with five postcanines and a variable small sixth incisor.

Ptomalestes: this monotypic genus has five to six fairly weak postcanines. The holotype is a well-preserved skull.

Pristerosaurus with a fairly large skull with weak canines and three small postcanines.

Zinnosaurus is a medium-sized scymnosaurine with five widely spaced weak incisors and two rather feeble postcanines.

Pristerognathinae

In 1895 Seeley described the first therocephalian under the name *Pristerognathus polyodon* – the holotype specimen being a poor weathered snout. Seeley had no difficulty in deciding that he had a fragment of an animal new

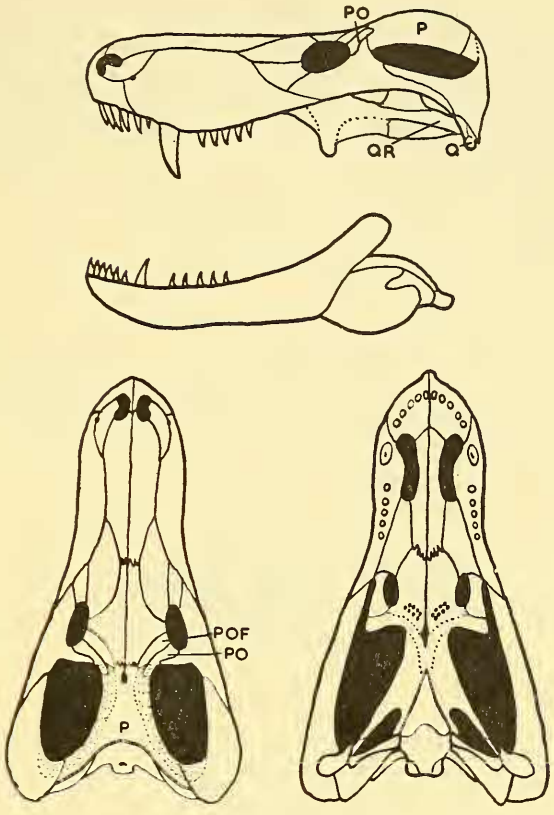

Fig. 20. Pristerognathid therocephalian represented by the skull of *Glanosuchus* in lateral, dorsal and ventral view.

to science. Why? Because hitherto no animal was known that had six upper and three lower incisor teeth and this was the only feature shown by his type. Broom, in 1904, described an even poorer snout as *Pristerognathus baini* because his specimen was somewhat smaller than Seeley's.

We now know that six upper incisors occur in a number of therocephalian species but this is not even a subordinal character, so that this feature by itself has no diagnostic value.

Pristerognathus polyodon is thus a *nomen dubium* and so is Broom's name—*P. baini*. I have transferred some of the later specimens which have been referred to the genus *Pristerognathus* to the genus *Pristerognathoides* of which a valid generic diagnosis can be given.

Two other described genera—*Hyorhynchus* and *Ictidopareia*—are both only identifiable as to family. My genus *Maraisaurus* appears to be based on a juvenile and is best included in the genus *Pristerognathoides*, and Brink's *Karowalteria* is based on a snout which falls within the range of the genus. *Alopognathus*, with

four species, contains moderate to fairly large pristerognathines with upper jaw dental formula I6 C1 PC4–6. The squamosal has an everted lateral edge. *Cynariognathus* with four species, is medium-sized with upper jaw dental formula I5–6, C1, PC6–9; the posterior incisors are smaller than the anterior ones, the canine is long and strong and the postcanines are fairly strong and form a closely set series. *Lycedops* is monotypic and has only four postcanines and the temporal fossa is short and broad.

Pristerognathoides, with six described species, has a dental formula I6, C1, PC5–6; the postcanines small, weak, and well spaced and the lateral edge of the squamosal is not everted.

Therioides is monotypic and known only from a single skull with some of the postcranial skeleton. Dental formula I6, C1, PC 6; the postcanines are small and slender and well spaced. The descending process of the squamosal is very deep so that the lower jaw articulation is situated far ventrally.

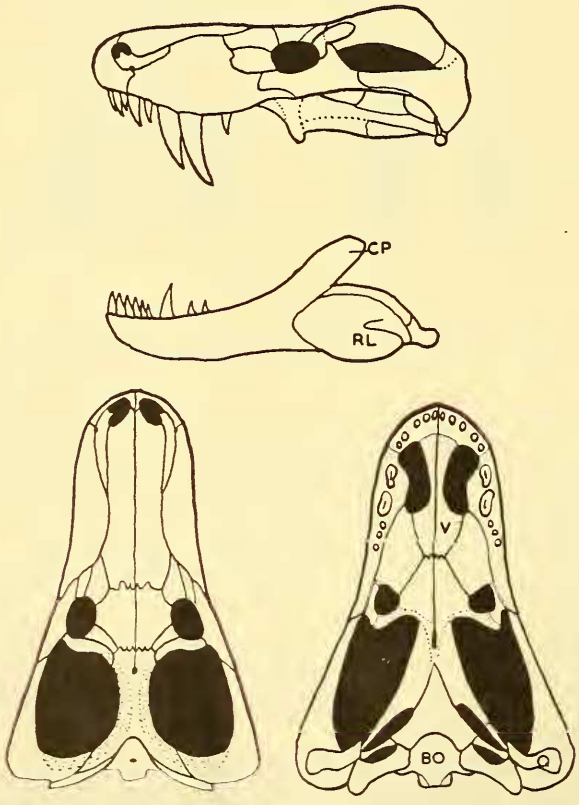

Fig. 21. Lycosuchid therocephalian represented by the skull of *Trochosaurus* in lateral, dorsal and ventral view.

Lycosuchidae

Early, fairly large Therocephalia with fairly broad flattened skulls with two functional canines in the maxilla, advanced broadened epipterygoid and low sagittal crest. Otherwise very similar to the pristerognathids. With four monotypic genera.

Hyaenasuchus – I6 C2 PC4
Lycosuchus – I5 C2 PC1
Trochorhinus – I5 C2 PC3
Trochosaurus – I5 C2 PC4

Alopecodontidae

Fairly small early Therocephalia of which the skulls are very inadequately known. The characteristic feature of the family is the presence of two small canines in the maxilla anterior to the single large canine. The family is composed of three monotypic genera based on five incomplete to very poor skulls.

Alopecideops gracilis with a very slender snout; dental formula I6, C3, PC 7.

Alopecodon with dental formula I7 C3, PC 7. The species *rugosus* and *minor* cannot be specifically distinguished from the holotype species *priscus*.

Pardosuchus whaitsi with dental formula I6, C3 PC5.

Scaloposauridae

From the *Tapinocephalus* zone a number of small forms are very inadequately known. They show the following scaloposaurid characters: small skulls with a long snout and slender lower jaw; the intertemporal region is fairly broad without a parietal crest; one to three canines and nine to ten postcanines. But the postorbital bar is complete and the dentary has a coronoid process.

Fig. 22. Scaloposaurid therocephalian represented by the skull of *Blattoidealestes* in lateral view.

The two forms under the names *Simorhinella baini* and *Ictidopareia brevirostris* should be considered *nomina dubia*, the former because it is based on an immature animal and the latter because the type is lost and it has never been adequately described. In *Blattoidealestes gracilis* some of the postcanines are triconodont.

The paratype of *Icticephalus polycynodon* is from this zone and Watson has shown that there exists a close affinity between this genus and *Scaloposaurus*.

Systematic List of the Tetrapods

AMPHIBIA
- LABYRINTHODONTIA
  - RHACHITOMI
    - Rhinesuchidae
      - *Rhinesuchus avenanti*
      - *Rhinesuchus whaitsi*
      - *Rhinesuchoides tenuiceps.*

REPTILIA
- ANAPSIDA
  - COTYLOSAURIA
    - DIADECTOMORPHA
      - Pareiasauridae
        - Bradysaurinae
          - *Bradysaurus angusta*
          - *Bradysaurus baini*
          - *Bradysaurus seeleyi*
          - *Bradysaurus strubeni*
          - *Embrithosaurus schwarzi*
  - CHELONIA?
  - EUNOTOSAURIA
    - Eunotosauridae
      - *Eunotosaurus africanus*
- LEPIDOSAURIA
  - EOSUCHIA
    - Millerettiformes
    - Millerettidae
      - *Broomia perplexa*
- SYNAPSIDA
  - PELYCOSAURIA
    - SPHENACODONTIA
      - Varanopsidae
        - *Anningia megalops*
        - *Elliotsmithia longiceps*

THERAPSIDA

ANOMODONTIA

DINOCEPHALIA

Anteosauridae

Anteosaurus magnificus
Paranteosaurus primus

Titanosuchidae

Jonkeria boonstrai
Jonkeria haughtoni
Jonkeria ingens
Jonkeria koupensis
Jonkeria parva
Jonkeria rossouwi
Jonkeria truculenta
Jonkeria vanderbyli
Titanosuchus ferox

Tapinocephalidae

Struthiocephalinae

Struthiocephalus whaitsi
Struthiocephaloides cavifrons
Struthiocephaloides duplessisi
Struthionops intermedius
Taurocephalus lerouxi

Moschopinae

Avenantia kruisvleiensis
Criocephalus vanderbyli
Delphinognathus conocephalus
Moschops capensis
Moschops koupensis
Moschops oweni
Moschops whaitsi

Riebeeckosaurinae

Riebeeckosaurus longirostris

Tapinocephalinae

Keratocephalus moloch
Mormosaurus seeleyi
Phocosaurus megischion
Tapinocephalus atherstonei

Styracocephalidae

Styracocephalus platyrhynchus

DICYNODONTIA
- Endothiodontidae
  - *Brachyuraniscus broomi*
  - *Brachyuraniscus merwevillensis*
  - *Brachyuraniscus reuningi*
  - *Broilius antjiesfonteinensis*
  - *Koupia koupensis*
  - *Pristerodon brachyops*
  - *Robertia broomiana*
- Dicynodontidae
  - *Dicynodon antjiesfonteinensis*
  - *Dicynodon gamkaensis*
  - *Dicynodon haughtonianus*
  - *Dicynodon jouberti*
  - *Dicynodon megalorhinus*
  - *Dicynodon pseudojouberti*
  - *Dicynodon schroederi*
  - *Dicynodon vanderhorsti*
  - *Oudenodon huenei*
- Dromasauridae
  - *Galeops whaitsi*

THERIODONTIA
- GORGONOPSIA
  - Galesuchidae
    - *Aelurosauroides watsoni*
    - *Broomiasaurus planiceps*
    - *Eoarctops vanderbyli*
    - *Galesuchus gracilis*
    - *Pachyrhinos kaiseri*
    - *Scylacognathus parvus*
  - Hipposauridae
    - *Hipposaurus boonstrai*
    - *Hipposaurus major*
- THEROCEPHALIA
  - Pristerognathidae
    - Scymnosaurinae
      - *Glanosuchus macrops*
      - *Ptomalestes avidus*
      - *Pristerosaurus microdon*
      - *Scymnosaurus ferox*
      - *Scymnosaurus major*
      - *Scymnosaurus watsoni*
      - *Zinnosaurus paucidens*

Pristerognathinae
Alopecognathus angusticeps
Alopecognathus angustioriceps
Alopecognathus megalops
Alopecognathus skinneri
Cynariognathus gallowayi
Cynariognathus paucioridens
Cynariognathus platyrhinus
Cynariognathus seeleyi
Lycedops scholtzi
Pristerognathoides minor
Pristerognathoides parvus
Pristerognathoides peyeri
Pristerognathoides roggeveldensis
Pristerognathoides vanderbyli
Pristerognathoides vanwyki
Theriodes cyniscus

Lycosuchidae
Hyaenasuchus whaitsi
Lycosuchus vanderrieti
Trochorhinus vanhoepeni
Trochosaurus major

Alopecodontidae
Alopecideops gracilis
Alopecodon priscus
Pardosuchus whaitsi

Scaloposauridae
Blattoidealestes gracilis
Icticephalus polycynodon.

Tapinocephalus Zone Faunas outside South Africa

Outside the main Karoo Basin in South Africa this fauna is known from only one other area in Africa, viz. in southern Rhodesia, where a *Criocephalus* and a therocephalian, probably pristerognathid, have been found.

From the rest of Gondwanaland no representatives of this fauna have as yet been recorded.

The only country which has as yet yielded a comparable fauna, which may be of the same age, is Russia. Here, the following families typical of the *Tapinocephalus* zone, viz. Anteosauridae, Tapinocephalidae and Pristerognathidae, have been recorded. No single genus occurs in both areas, but the Russian *Doliosauriscus* is very close to our *Anteosaurus* and the Russian *Ulemosaurus* is very

similar to our *Moschops*. For the rest there are considerable differences between the two faunas, the most important being the presence of more primitive forms in Russia, which incline one to the view that the Russian fauna of Zone I and possibly of Zone II are somewhat older.

COMPARATIVE TABLE OF THE FAUNAS OF THE *Tapinocephalus* ZONE OF SOUTH AFRICA AND ZONES I AND II OF THE RUSSIAN SUCCESSION

	GENERA		
	Tapinocephalus zone South Africa	Zone I Russia	Zone II Russia
Subclass: Anapsida			
Order: Cotylosauria			
Suborder: Captorhinomorpha			
Family: Captorhinidae	—	—	*Hecatogomphius*
Suborder: Didectamorpha			
Infra-order: Pareiasuria			
Family: Rhipaeosauridae	—	—	*Rhipaeosaurus*
	—	—	*Leptoropha*
Family: Pareiasauridae	*Bradysaurus*	—	—
	Embrithosaurus	—	—
Infra-order: Procolophonia			
Family: Nyctiphruretidae	—	—	*Nyctiphruretus*
	—	—	*Nycteroleter*
	—	—	*Nyctiboetus*
Order: Chelonia?			
Suborder: Eunotosauria			
Family: Eunotosauridae	*Eunotosaurus*	—	—
Subclass: Lepidosauria			
Order: Eosuchia			
Suborder: Millerettiformes			

	GENERA		
	Tapinocephalus zone South Africa	Zone I Russia	Zone II Russia
Family: Millerettidae	*Broomia*	—	—
Family: Mesenosauridae	—	—	*Mesenosaurus*
Subclass: Synapsida			
Order: Pelycosauria			
Suborder: Sphenacondontia			
Family: Varanopsidae	*Anningia*	—	—
	Elliotsmithia	—	—
Suborder: Edaphosauria			
Family: Phreatosauridae	—	*Phreatophasma*	—
	—	*Phreatosuchus*	—
	—	—	*Phreatosaurus*
Family: Caseidae	—	—	*Ennotosaurus*
Order: Therapsida			
Suborder: Eotitanosuchia			
Family: Eotitanosuchidae	—	*Eotitanosuchus*	—
	—	*Biarmosaurus*	—
	—	*Biarmosuchus*	—
	—	—	*Phthinosaurus*
	—	—	*Phthinosuchus*
Suborder: Anomodontia			
Infra-order: Dinocephalia			
Family: Brithopidae	—	*Archaeosyodon*	—
	—	*Chthomalopus*	—
	—	—	*Brithopus*
	—	—	*Notosyodon*
	—	—	*Syodon*
	—	—	*Titanophoneus*
Family: Anteosauridae	*Anterosaurus*	—	—
	Paranteosaurus	—	—

	GENERA		
	Tapinocephalus zone South Africa	Zone I Russia	Zone II Russia
	—	—	*Admetophoneus*
	—	—	*Deuterosaurus*
	—	—	*Doliosauriscus*
Family: Titanosuchidae	*Jonkeria*	—	—
	Titanosuchus	—	—
Family: Tapinocephalidae			
Subfamily: Struthiocephalinae	*Struthiocephalus*	—	—
	Struthiocephaloides	—	—
	Struthionops	—	—
	Taurocephalus	—	—
Subfamily: Moschopinae	*Avenentia*	—	—
	Criocephalus	—	—
	Delphinognathus	—	—
	Moschops	—	—
	—	—	*Ulemosaurus*
	—	—	*Mnemeiosaurus*
Subfamily: Riebeeckesaurinae	*Riebeeckosaurus*	—	—
Tapinocephalinae	*Keratocephalus*	—	—
	Mormosaurus	—	—
	Phocosaurus	—	—
	Tapinocephalus	—	—
Family: Styracocephalidae	*Styracocephalus*	—	—
Family: Estemmenosuchidae	—	*Anoplosuchus*	—
	—	*Estemmenosuchus*	—
	—	—	*Molybdopygus*
Infraorder: Dicynodontia			
Family: Otsheriidae	—	*Otsheria*	—
Family: Venyukovidae	—	—	*Venyukovia*
Family: Endothiodontidae	*Brachyuraniscus*	—	—
	Broilius	—	—
	Koupia	—	—
	Robertia	—	—

	GENERA		
	Tapinocephalus zone South Africa	Zone I Russia	Zone II Russia
Family: Dicynodontidae	*Dicynodon*	—	—
	Oudendon	—	—
Family: Dromasauridae	*Galeops*	—	—
Suborder: Theriodontia			
Infra-order: Gorgonopsia			
Family: Galesuchidae	*Aelurosauroides*	—	—
	Broomisaurus	—	—
	Eoarctops	—	—
	Pachyrhinos	—	—
	Scylacognathus	—	—
	—	—	Unnamed
Family: Hipposauridae	*Hipposaurus*	—	—
Infra-order: Therocephalia			
Family: Pristerognathidae	—	—	*Porosteognathus*
	Glanosuchus	—	—
	Ptomalestes	—	—
	Pristerosaurus	—	—
	Scymnosaurus	—	—
	Zinnosaurus	—	—
	Alopecognathus	—	—
	Cynariognathus	—	—
	Pristerognathoides	—	—
	Theriodes	—	—
Family: Lycosuchidae	*Hyaenosuchus*	—	—
	Lycosuchus	—	—
	Trochorhinus	—	—
	Trochosaurus	—	—
Family: Alopecodontidae	*Alopecideops*	—	—
	Alopecodon	—	—
	Pardosuchus	—	—
Family: Scaloposauridae	*Blattoidealestes*	—	—
	Icticephalus	—	—

The (3) suborders Anapsida, Lepidosauria and Synapsida are common to the three zones of South Africa and Russia.

The (4) orders Cotylosauria, Eosuchia, Pelycosauria and Therapsida are common to the three zones but the order Chelonia? is unrepresented in Russia.

The (4) sub-orders Diadectamorpha, Millerettiformes, Anomodontia and Theriodontia are common to the three zones, but the (2) sub-orders Eunotosauria and Sphenacodontia are unrepresented in Russia and the (3) sub-orders Captorhinomorpha, Edaphosauria and Eotitanosuchia are absent from South Africa.

The (5) infra-orders Pareiasauria, Dinocephalia, Dicynodontia, Gorgonopsia and Therocephalia are present in South Africa as well as in Russia. The (1) infra-order Procolophonia was unrepresented in South Africa during this period.

Only the (3) families Anteosauridae, Tapinocephalidae and Pristerognathidae are common to the two countries. Nine families occur only in Russia and 14 only in South Africa.

Russia and South Africa have no genera in common. Of the 81 genera here recognized as firmly established South Africa has 55 and Russia 26. But *Ulemosaurus* is very near to *Moschops* and *Doliosauriscus* is very near to *Anteosaurus*.

Origin of the *Tapinocephalus* Zone Reptilian Fauna

It is abundantly clear that the fossil remains at present known from the rocks of the *Tapinocephalus* zone represent but a small part of the fauna which must have lived during these times. Of the invertebrates we know next to nothing and of the fish and amphibians we know little. Do the reptiles we know fully represent this group? How many others lived in the Karoo at this age of whom no remains have as yet been found or were not preserved as fossils?

The oldest reptiles of Carboniferous and Lower Permian age comprise the orders Cotylosauria, Mesosauria, Protorosauria and Pelycosauria. Of these, the Mesosauria did not survive beyond the Carboniferous. The Protorosauria, which elsewhere survived to the Jurassic, have no representatives in the *Tapinocephalus* zone. Of the stem group of the reptiles – the Cotylosauria – only the bradysaurines occur in the *Tapinocephalus* zone and here form a well-developed population of large herbivores. Of the pelycosaurs a few 'Last of the Mohicans' lived into *Tapinocephalus* zone times. One of the oldest eosuchians is present in this zone.

It is the newly evolved Therapsida which form the overwhelming, dominant group in the fauna of the *Tapinocephalus* zone. Whence came these therapsids – parvenus and immediately dominant?

In the Karoo, rocks of the Ecca Series underlie those of the *Tapinocephalus* zone conformably and one would expect these to contain the immediate forebears of the reptiles of the *Tapinocephalus* zone. Hitherto the Ecca has not yielded a single reptilian specimen.

Why?

It is possible that during Ecca times the Karoo Basin was inhabited by an ancestral fauna but that for some reason no remains of these animals were preserved as fossils.

What were the factors that precluded preservation? Could it be that the nature of the sedimentation during Ecca times was such that fossilization was made impossible? In the western part of the Karoo Basin there is nothing to indicate any radical difference in the sedimentation processes which formed the rocks of the Ecca beds and those forming the rocks of the *Tapinocephalus* zone. In fact the dividing line between these beds stipulated by stratigraphers is an arbitrary one and lies below the first band of purple mudstones encountered in the column. Above and below this arbitrary line the constituent mudstones and sandstones were deposited in a similar way, viz. by fresh water dropping its load of similar fine silt or coarser sand, according to the rate of flow, in depressions in a general low-lying flood plain. If the hard parts of the reptiles were included and subsequently mineralized above the arbitrary line they should, if present, also have been entombed and preserved below this line. The only reasonable conclusion is thus that during Ecca times the Karoo Basin was not inhabited by a reptilian fauna.

The presence of purple mudstones above the arbitrary line and their absence below the line may indicate that, although the mechanical nature of the sedimentation was similar in both cases, there was in fact some other difference. The green-blue colour of the Ecca mudstones is due to the presence of the lower oxides of iron and the purplish colour in the purple bands of the *Tapinocephalus* and higher zones is due to the presence of the higher red oxides of iron. An increase in temperature is known to be conducive to the further oxidation of iron salts. It is thus reasonable to assume that periods of higher temperature occurred in *Tapinocephalus* zone times and that this made reptilian life possible and that reptiles were absent in the Karoo Basin during Ecca times because the temperature was too low for reptile life.

In the north-eastern part of the Karoo Basin the middle portion of the Ecca beds has yielded a well-developed flora which was also the source of the extensive and massive seams of coal. Did this flora also live in a moist and cold climate? In the rest of Gondwanaland, beds of Ecca age have also proved barren of reptiles.

In the lower beds of Dwyka age, the presence of *Mesosaurus* in various parts of Gondwanaland shows that at this early age the reptiles had developed at least one group probably closely related to the therapsids and far from primitive. It would thus appear that the stem-reptiles of the Therapsida lived well down in Carboniferous times.

With no ancestors in Gondwanaland, one turns to the northern hemisphere in the search for the forebears of the *Tapinocephalus* zone fauna of the Karoo.

The presence of a comparable fauna in Zones I and II of the Russian succession makes this imperative. The presence of some forms in Russia more

primitive than those of the Karoo indicates that the Russian beds may lie nearer to the home of the ancestors.

However, the Lower Permian of the northern hemisphere has as yet yielded no therapsids so that we still do not know any of the first forms of this order.

Between the therapsids and the morphologically more primitive pelycosaurs and cotylosaurs of the northern hemisphere we still have a morphological gap.

The pelycosaurs and cotylosaurs of the Lower Permian of Europe and America would have had the first therapsids as contemporaries, and could thus not have been their direct ancestors.

Moreover, we know of no Lower Permian pelycosaur that is unspecialised enough to have been an ancestor of any known therapsid.

The pelycosaurs known can be considered as an offshoot of the direct therapsid line.

This pushes the origin of the therapsids another step back, viz. to the more primitive cotylosaurs of the Carboniferous.

Descendants of the Fauna of the *Tapinocephalus* Zone

In Africa, the conformably overlying *Endothiodon* and *Cistecephalus* zones, comprising the Upper Permian, have the following direct descendants:

The bradysaurines gave rise to the pareiasaurines.
The varanopsids peter out.
The Dicynodontia really start to flourish and so do the Gorgonopsia.
The Therocephalia develop new families and give rise to the first cynodonts.
Of the eosuchians the millerettids continue and two other families arise.
All these groups spread out to East or Central Africa.

The comparable Russian faunas of Zones I and II evolved on similar lines but less robustly. Some pareiasaurs and dicynodonts spread to western Europe and dicynodonts to Indo-China.

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